THE AMPHIPOD SUPERFAMILY DEXAMINOIDEA ON THE NORTH AMERICAN PACIFIC COAST; FAMILIES ATYLIDAE AND DEXAMINIDAE: SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY.

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ABSTRACT

Based mainly on study material from North American Pacific coastal marine waters (from the Bering Sea region to northern California), this study treats the systematics and distributional ecology of regional family and subfamily members of the gammaridean amphipod superfamily Dexaminoidea. Cluster analysis of 22 component genera supports subdivision of this taxonomically difficult group into two principal families, the primitive, thin bodied Atylidae, and the more advanced, broad bodied Dexaminidae. Family Atylidae encompasses the subfamilies Atylinae Leach 1814 (revised status); Anatylinae Bulycheva 1955 (revised status), Lepechinellinae Schellenberg,. 1926 (revised status); and **Nototropiinae,** new subfamily. Family Dexaminidae here encompasses subfamily Dexamininae Leach, 1814 (revised status); Prophliantinae (Nicholls, revised Barnard, 1970); **Dexaminoculinae**, new subfamily, and **Polycheriinae**, new subfamily.

Material from the study region contains representatives of both families and three component subfamilies. Within subfamily Atylinae are newly described and figured ***Atylus georgianus***, new species and ***A. borealis,*** new species. Newly recorded from the study region and/or refigured are: *Atylus atlassovi* (Gurjanova, 1951), *A. bruggeni* (Gurjanova, 1938), *A. collingi* (Gurjanova, 1938), and *A. levidensus* Barnard, 1954, *A. tridens* (Alderman, 1936), and the type species *A. carinatus* J. C. Fabricius, 1783. Rediagnosed and refigured from the western Pacific region are *Atylus ekmani* Gurjanova, 1938 and *A. rylovi* Bulycheva, 1952. Based on analysis of the literature and records from the western Pacific, subfamily Anatylinae here encompasses *Anatylus pavlovskii* Bulycheva, 1955, and *Kamehatylus japonicus* (Nagata, 1961). Subfamily Nototropiinae contains the western Pacific *Nototropis* sp. (cf. *guttatus* Costa) and the abyssal species, *Atylus aberrantis* (Barnard, 1962), here transferred from subfamily Lepechinellinae in the monotypic new genus ***Aberratylus.***

Within family Dexaminidae, subfamily Polycheriinae is moderately well represented in amphi-North Pacific waters. Newly described and figured are ***Polycheria carinata,*** new species, and ***P. mixillae,*** new species, and *Polycheria osborni* Calman, 1898 is redescribed. Subfamily Prophliantinae, is represented in Asiatic Pacific coastal waters by about a dozen described species, but in the North American study region, the sole species identified to date is *Guernea reduncans* (J. L. Barnard, 1958). Subfamily Dexamininae is well represented in the western North Pacific by species of *Paradexamine* but is absent from the eastern North Pacific.

Biogeographically, within family Atylidae, members of the primitive subfamily Atylinae are endemic to the North Pacific region. From there, members of the more advanced Nototropiinae and Anatylinae have apparently radiated into the Indo-Pacific and former tethyan warm-water regions. Members of subfamily Lepechinellinae, having a common ancestor with the Nototropiinae, have become abyssal. Nearly all members of the more advanced family Dexaminidae are warm-temperate and tropical but a few species of the most advanced subfamily, Polycheriinae, have penetrated into the cold temperate North Pacific, apparently from two different sources. The sole North American Pacific prophliantin species appears more closely related to counterparts in the North Atlantic region than to prophliantins of the western North Pacific.

Except for the abyssal Lepechinellinae, most dexaminoideans are littoral-sublittoral in depth range and all are exclusively marine. In life style, they mainly nestle on the bottom, in sea grass clumps, coral clusters, empty shells, or in pits excavated in the tests of colonial invertebrates, but the Prophliantinae apparently burrow in soft sediments. Species densities are seldom high and total biomass is low, presumably with little significance in regional food energy cycles. The group may be considered a specialized relict offshoot of early gammaroidean ancestral types, from which may have also evolved the closely related, but ecologically more successful, ampeliscoidean amphipods that are tube-dwelling and deposit-feeding in soft sediments, world-wide.

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INTRODUCTION

The superfamily Dexaminoidea encompasses a group of benthic nestling amphipods that occur mainly on hard substrata in tropical and warm temperate regions of the world. The number of described species is relativley small (< 200), and populations are generally of low density. However, morphological diversity within the group is relatively high (cf. Gammaroidea with 5 times the number of species), possibly reflecting the wide variety of solid (and some sedimentary) substrata on which various subgroups of Dexaminoidea have been modified for existence.

The animals are characterized by variously carinated or dorsally processiferous bodies, fused urosome segments 2 & 3, a tendency to prehensility (subchelation) of peraeopods 3-7, and a reproductive life style that involves mating freely in the water column. The gnathopods are weakly (or not) sexually dimorphic, but in the type genus *Dexamine* and close relatives, the anterior margin of the propod of gnathopod 1 (in the male) bears a characteristic notch or sharp excavation, of presumed (but unknown) reproductive function. Although basically free-living, with well developed peraeopods, pleopods, and tail fan, the animals are typically slow-moving, even sedentary, in vegetative life style. Most species are deposit or tryptон feeders, frequently employing specialized setae of the antennae and anterior peraeopods to rake in organic food material, from a nearly fixed position on the bottom. Members of the specialized genus *Polycheria* are commensal on the tests of colonial tunicates and sponges where they live "upside down" in pits excavated in the surface of the host. However, unlike the closely related ampeliscoideans, of similar "upside-down" feeding style, dexaminoideans lack spinning glands in the anterior peraeopods and are incapable of tube building.

The classification of the group within suborder Gammaridea has gone through an early period of stability, followed by a recent period of relative instability. Early workers (e.g Sars,1895; Stebbing,1908) maintained the atylids and dexaminids as separate families, and recognized the close similarity of atylids to the basic "Gammaridae" amphipod type. Such stability was extended to the Lepechinellidae (Stebbing, 1908) and the Prophliantidae (Nicholls, 1939) by more recent major workers (e.g. Gurjanova ,1951; Barnard, 1969a). Soon afterwards, however, a developing trend to fusion of related higher taxa, led to submergence of all dexaminid groups within family Dexaminidae (e.g. Bellan-Santini, 1982) or to formal creation of a new superfamily group, Dexaminoidea, in which family levels of distinction could be maintained (e.g. Bousfield, 1979, 1982).

Dexaminoidean amphipods are among the few regional North Pacific gammaridean groups that have received significant taxonomic attention. Within the Dexaminidae proper, *Polycheria osborni* was described from California by Calman(1898). Within family Atylidae, the genus *Atylus* had been unknown from the Pacific coast of North America prior to Alderman's (1936) description of *A. tridens* from California. That record was closely followed by Gurjanova's (1938) description of *A. collingi* from eastern Siberia and Bering sea regions, and by J. L. Barnard's (1956) description of *A. levidensus* from California. Based on CMN material collected along the Pacific coast of Canada, 1955 - 1959, Mills (1962) provided illustrated descriptions, keys, and distributional data on those three species from the coastal marine region of British Columbia. Further records from California were added by Barnard (1962, 1969b and Cadien (1991). Barnard (1975), and Staude (1987) included dexaminids in keyed and illustrated popular regional works and Austin (1985) summarized records from the cold temperate northeast Pacific region . Within family Prophliantidae, *Guernea (Prinassus) reduncans* Barnard had been recorded widely along Californian coasts by Barnard (1958, 1969b, 1972) and Cadien (1991). The biology of *Polycheria osborni* was studied in detail by Skogsberg & Vansell (1928), and some members of the Lepechinellidae were recorded from the eastern Pacific abyss by Barnard (1967, 1972).

In the western North Pacific, the early work of Gurjanova (1938), and Stephensen (1944) was encompassed by Gurjanova (1951). Subsequently Bulycheva (1952, 1955) proposed further species of *Atylus*, *Polycheria* and *Anatylus*; and Birstein & Vinogradov (1955) recorded an abyssal lepechinellid. From Japanese waters Nagata (1961) described the aberrant *Atylus japonicus*. The more recent work of Gamo (1981) on *Lepechinella*, of Hirayama (1984a,b, 1984, 1986) on species of *Paradexamine*, *Polycheria*, *Guernea*, and *Atylus*, and Ishimaru (1987) on *Guernea*, and others, has been summarized most usefully in a catalogue of dexaminid amphipods of Japan by Ishimaru (1994).

Dexaminid systematics and distribution have been treated comprehensively and most usefully by Barnard & Karaman (1991). However, the lumping of diverse subgroups within one family, with recognition of only one additional subfamily and no superfamilies, and the use of too few, or phyletically non-significant, character states in diagnoses and keys, tends to create problems of inconsistency in taxonomic analysis and an unwieldiness of classification that may also apply elsewhere within gammaridean classification (e.g. within family Eusiridae). Our purpose here is to (1) develop new basic taxonomic information and analytical criteria from a study of the present North Pacific material; (2) incorporate this information with previous knowledge as a basis for numerical analysis of natural relationships between higher taxonomic categories, and (3) modify existing classifications in a manner that more consistently reflects distributional, ecological, and behavioural, as well as taxonomic and phyletic, differences between the subgroups.

The authors have recently examined extensive new material in the amphipod collection of the Canadian Museum of Nature (CMN), Ottawa, that supplements the earlier material of Mills (1961), and material from the Bering Sea region (Peter Slattery expeditions) and elsewhere. Station lists for CMN museum material, 1955 - 1980, are provided

by Mills (1962), Bousfield (1958, 1963, 1968), Bousfield and McAllister (1963), and Bousfield and Jarrett (1981).

This report provides an extensive review of the systematics, distributional ecology of the dexaminoidean fauna from the North American Pacific coastal marine region and relates it phyletically and biogeographically to counterpart faunas of the western North Pacific and elsewhere in the world.

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SYSTEMATICS

DEXAMINOIDEA Leach (revised Bousfield)

Dexaminoidea: Bousfield, 1979: 350.—Bousfield, 1982: 277.—Bousfield, 1983: 263.—Schram, 1986: 180.
Dexaminidae Barnard, 1970: 161.—Ishimaru, 1987: 1412.—Barnard & Karaman, 1991: 260.

Families: 1. Atylidae G. O. Sars, 1882: 26. Includes subfamilies Atylinae Sars (revised status); Lepechinellinae Schellenberg 1926 (revised status); Nototropiinae, new subfamily; and Anatylinae Bulycheva, 1955 (revised status).

2. Dexaminidae Leach, 1813/14: 432. Includes subfamilies Dexamininae Leach (revised status); Polycheriinae, new subfamily; Dexaminoculinae, new subfamily; and Prophliantinae Nicholls, 1939 (revised status, Barnard 1970).

Diagnosis (after Bousfield, 1982): Rostrum present, variable. Body (especially urosome) usually with mid-dorsal, and often dorso-lateral, carinations or teeth. Urosome segment 1 dorsally carinate. Urosome segments 2 & 3 coalesced, often dorsally carinate. Sexual dimorphism pronounced in eyes, antennae, uropod 3, and coxal gills, but weakly expressed in gnathopod 1. Eyes pigmented and multi-faceted, lacking in bathyal forms. Antennae variable; peduncles of flagella (male) armed with brush setae. Antenna 1, peduncular segment 2 usually longer than 1; segment 3 short; accessory flagellum minute or lacking. Antenna 2 trending to shortening (female); flagellum elongate, non-calceolate (male).

Mouthparts trending to modification. Upper lip entire. Lower lip, inner lobes variously developed. Mandibular molar triturative, but trending to reduction; left lacinia basically 5-dentate; palp various, weak or lacking. Maxilla 1, inner plate 0-8 setose, outer plate 7-11 spinose; palp often 1-segmented. Maxilla 2, inner plate the smaller, trending to loss of marginal setae. Maxilliped, outer plate large, inner plate and palp trending to reduction in size and loss of setae.

Coxal plates 1-4 medium to small, often notched or incised below; coxa 5 strong, often antero-lobate. Gnathopods small, weakly subchelate (palms convex), generally dissimilar in form. Gnathopod 1, propod may be distinctively sexually dimorphic.

Peraeopods 3 & 4 subequal, or peraeopod 4 smaller, trending to shortening of segment 5. Peraeopods 5-7 variable in form and size, bases unequally broad, trending to linearity; segment 5 variable; segment 6 and dactyl trending to subchelation.

Pleopods usually strong, especially in male. Uropods 1 & 2, rami unequal, lanceolate, apically spinose. Uropod 3 aequiramous; rami lanceolate, outer ramus 1-segmented, margins setose in male, often so in female.

Telson bilobate, lobes variously fused basally, apices spinose, notched or finely crenulated.

Coxal gills sac-like, on peraeopods 2-7(6), often pleated or phylloform, especially in male. Brood lamellae medium broad or strap-like, trending to linearity.

Reproductive Life Style: synchronous, mating freely in water column (presumed from morphology - nearly all members).

Taxonomic and Biogeographic Commentary: Cluster analysis of all 22 generic-level taxa within superfamily Dexaminoidea recognizedhere (p. 56) supports the validity of the family and subfamily components listed above, and detailed in the following systematic accounts. The most primitive subfamily, Atylinae is endemic to the boreal-subarctic North Pacific; others are components of mainly Indo-Pacific faunas marginally present in this region.

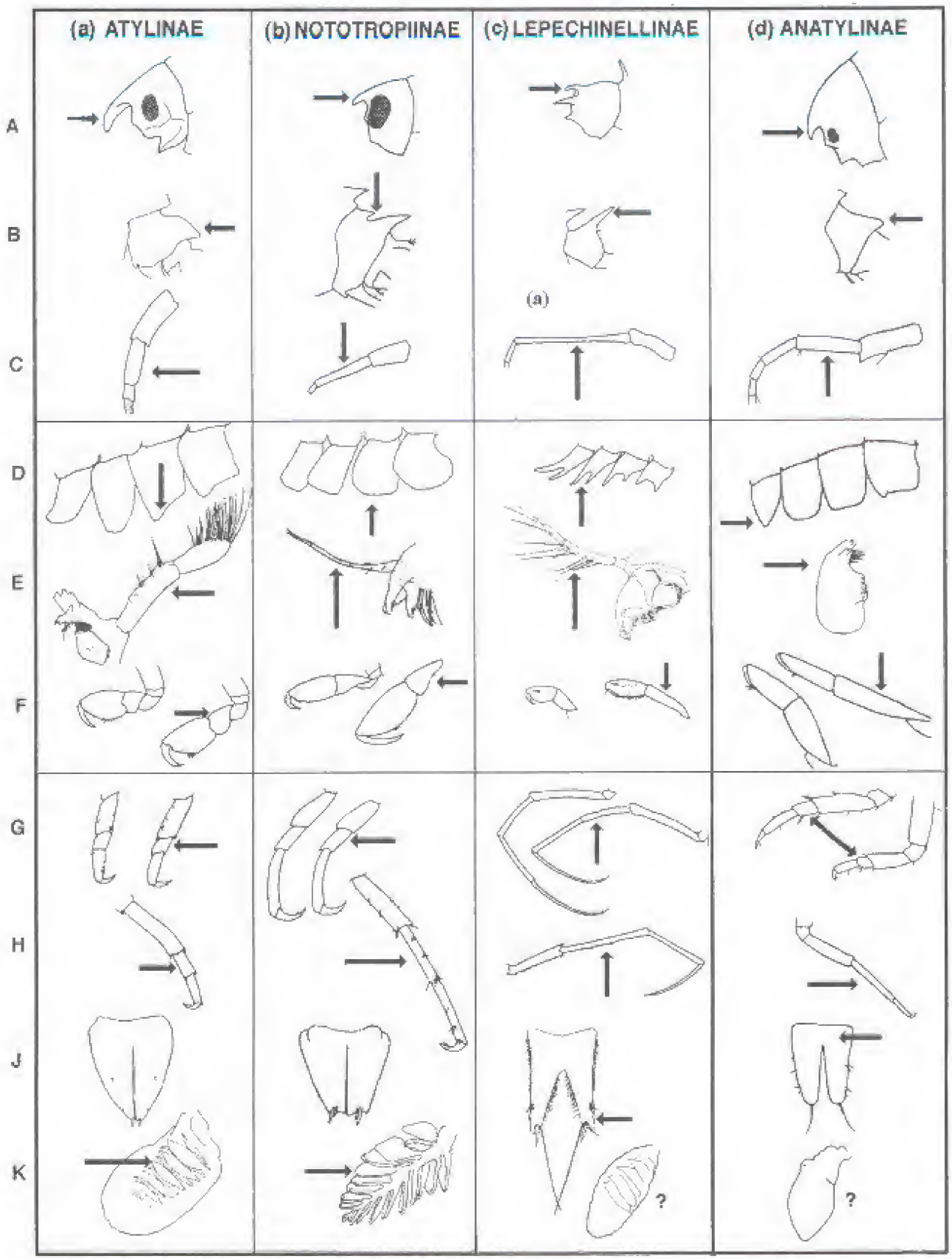

FIG. 1. ATYLIDAE: TYPICAL CHARACTER STATES

A - Rostrum; B - Urosome 1; C - Antenna 1; D - Coxa 1; E - Mandible; F - Gnathopod 1; G - Peraeopods 3-4; H - Peraeopods 5-7; J - telson; K - coxal gills 2-5; (from text plates)

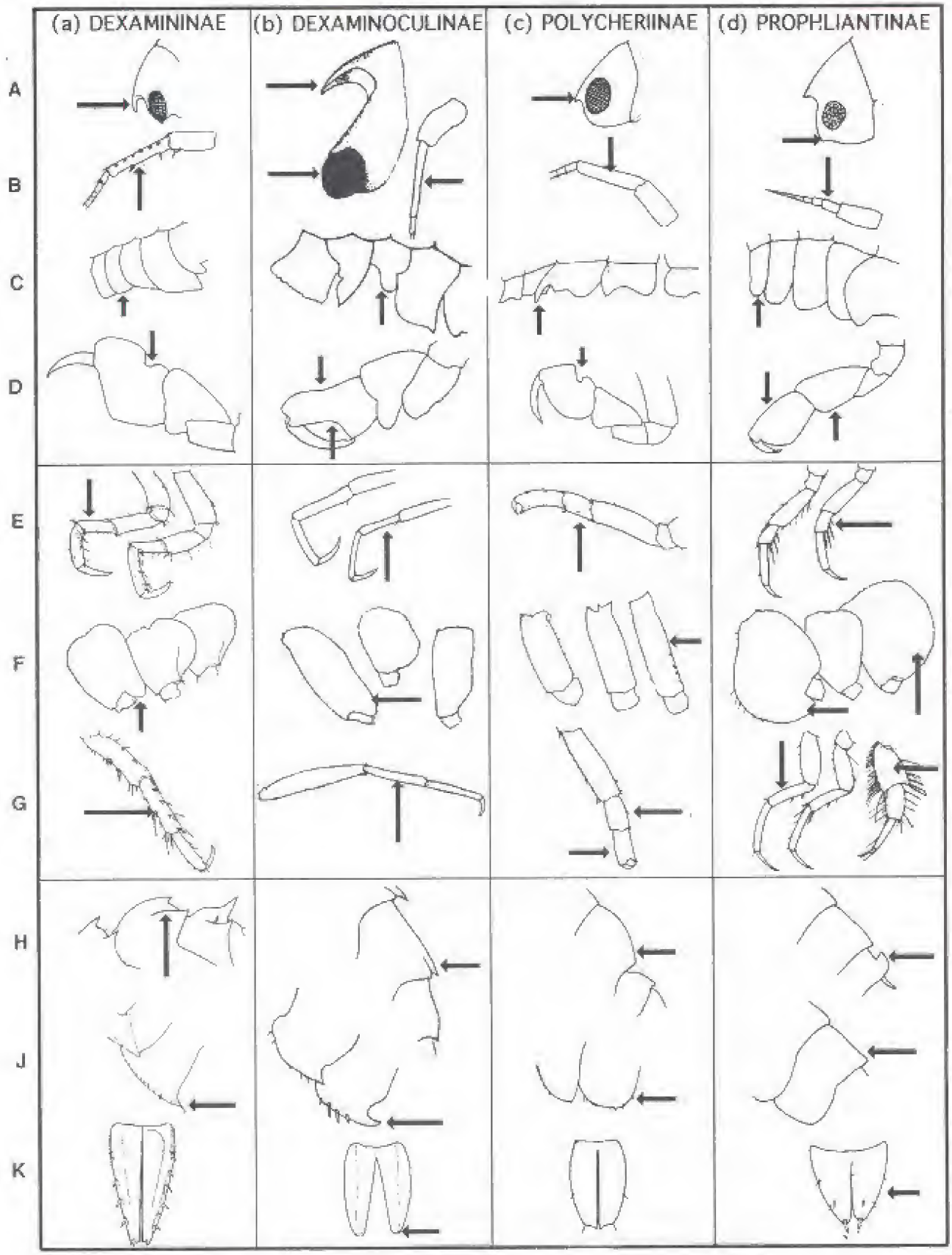

FIG. 2. DEXAMINIDAE: TYPICAL CHARACTER STATES

A - Rostrum; B - Antenna 1; C - Coxa 1-4; D - Gnathopod 1 (male); E - peraeopods 3-4; F - peraeopods(5-7 bases) G - peraeopods 5-7 (distal); H - abdomen dorsum; J - Pleon plates 2-3; K - telson (from text plates)

KEY TO WORLD FAMILIES OF DEXAMINOIDEA

1. Body slender; antennae medium-long; antenna 2 not reduced (female); mandible usually with palp; maxilla 1, palp 2-segmented; maxilliped almost normal; coxa 5 shallow, strongly antero-lobate . **Atylidae.**

—Body short, broad; antenna often short, A2 shortened (female): mandible lacking palp; maxilla 1, palp 1-segmented; maxilliped palp distinctly reduced; coxa 5, broad, aequilobate, usually deep . . **Dexaminidae.**

Atylidae G. O. Sars

Atylidae: G. O. Sars, 1882: 26.—Stebbing, 1906: 327.—Barnard, 1969a: 161.—Bousfield, 1982: 277.
Anatylidae: Bulycheva, 1955: 204.—Bousfield, 1982: 277
Dexaminidae (part): Barnard, 1970a: 164.—Bellan-Santini, 1983: 212.—Barnard & Karaman, 1991: 260.

Type Genus: *Atylus* Leach, 1815: 21. (Type *A. carinatus* Fabricius 1793).

Diagnosis: Body slender, laterally compressed. Posterior peraeonand pleon var-iously carinate or smooth. Urosome 1 mid-dorsally carinate. Rostrum various, usually medium to strong. Antennae not short, antenna 2 the longer. Antenna 1, peduncular segment 2 subequal to segment 1, often longer; accessory flagellum present, minute.

Lower lip, inner lobes usually lacking. Mandible with palp (few exceptions), triturating molar, 5-dentate left lacinia, and several blades in spine row. Maxilla 1, palp 2-segmented. Maxilla 2 normal, margins setose. Maxilliped inner plates normal, apex spinose; palp strong.

Coxae 1-4 various, lower margins may be acute, occasionally incised, 2 & 3 deepest, 1 less deep. Gnathopods 1 & 2 weakly subchelate, weakly sexually dimorphic; carpus various, often slender.

Peraeopods 3 & 4, segment 5 usually much shorter than segments 4 & 6 and dactyls not elongate (except in Lepechinellinae). Peraeopods 5-7 not elongate, bases variously expanded and lobate below, somewhat dissimilar in form; segment 5 various. Pleopods various, usually strong. Pleon plates 1-3, hind corners squared or acuminate. Uropod 3, rami lanceolate, margins setose (esp, male) or spinose. Telson lobes normal, short to medium, fused basally.

Coxal gills often pleated or plaited. Brood plates broad.

Taxonomic Remarks: The family Atylidae is here subdivided into 4 subfamilies as diagnosed below. They are separated on character states of the key (below) for which illustrations are provided in Fig. 1, and in pertinent sections of the text.

Subfamily Atylinae Boeck (revised status)

Atylinae Boeck, 1876: 320.
Atylidae Stebbing, 1906: 327.— Gurjanova, 1951: 678.—Barnard, 1969: 163.
Dexaminidae (part) Bellan-Santini, 1982: 212.—Barnard & Karaman, 1991: 260.

Type genus: *Atylus* Leach, 1815.

Diagnosis: Generally medium to large atylids (5-40 mm). Rostrum usually large. Posterior peracon, pleon, and

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KEY TO SUBFAMILIES OF ATYLIDAE

1. Peraeopods 3 and 4 closely subequal in size; peraeopods 5-7, segment 5 distinctly shorter than segments 4 & 6; antenna 1, peduncular segment 1 shorter than peduncular segment 2 (always, in female) . . . . . **Atylinae** (p. 8)
—Peraeopod 4 distinctly shorter than peraeopod 3 (in distal segments); peraeopods 5-7 segment 5 not distinctly shorter than segments 4 & 5; antenna 1 peduncular segment 2 variously longer than segment 1 . 2.

2. Eyes lacking; anterior head lobe strongly bifid; peraeopods and dactyls very slender, elongate; telson lobes short, diverging distally . . . . . **Lepechinellinae** (p. 31)
—Eyes present; anterior head lobe blunt or slightly emarginate; peraeopods and dactyls normal length and thickness; telson lobes normal, converging distally . . . . . 3.

3. Pleon segments 1-3 not carinate; urosome 1 with simple mid-dorsal tooth; mandible lacking palp; uropod 3, rami short, margins spinose; peraeopod 5, basis not lobate below; gills simple . **Anatylinae** (p. 32)
—Pleon segment 1-3 usually carinate mid-dorsally; urosome 1 with tooth and notch; mandible with palp (weak); uropod 3, rami lanceolate, margins setose (esp. male); peraeopod 5, basis with lower hind lobe; gills phylliform . . . . . **Nototropiinae** (p. 28)

urosome usually dorsally carinate. Antennae large, setose.

Mouthparts basic. Mandibular molar, spine row, and palp well developed. Maxilla 1, inner plate separate, apically setose. Maxilla 2, plate margins setose. Maxilliped normal, plates and palp well developed.

Coxal plates 1-4 medium, lower margins often weakly incised or subacute anter-iorly. Gnathopods medium, subsimilar, weakly sexually dimorphic.

Peraeopods 3 & 4 subsimilar in form and size; segment 5, distinctly shorter than segments 4 & 6. Peraeopods 5-7, bases broadened; segment 5 variously shorter than segments 4 & 6. Peraeopod 5, basis, hind lobe weak, not produced below. Peraeopod 7, basis very broad, posterior lobe present, acute or rounded below.

Pleopods strong. Uropod 3, rami strong, margins spinose and usually setose (both sexes). Telson lobes medium to large, with apical spine(s). Anterior coxal gills usually pleated, especially in males.

Taxonomic and Distributional Commentary: The subfamily Atylinae presently contains a single genus, *Atylus*, encompassing about a dozen species, almost all endemic to the boreal and subarctic North Pacific region. The range of morphological variation is sufficiently great that recognition of internal groupings (e.g. the *collingi* subgroup) may eventually justify subgeneric recognition.

The principl features of subfamily Atylinae are contgrasted with those of other subfamilies of Atylidae in Figure 1. In summary: (referred to in following text, where pertinent).

Atylus Leach, 1815

Atylus Leach, 1815: 21.—Mills, 1961: 17 (key).—Barnard, 1956: 38.—J. L. Barnard, 1969a: 163.—J. L. Barnard, 1970a: 164.—Barnard & Karaman, 1991: 262 (part).
Nototropis Gurjanova, 1951: 680 + key. (part)
non *Anatylus* Bulycheva, 1955: 205.—Tzvetkova, 1967: 391.
non *Kamehatylus* Barnard, 1970b: 93.

Type Species: *Gammarus carinatus* J. C. Fabricius 1793, monotypy.

Species: *A. atlassovi* (Gurjanova, 1951); *A. borealis*, new species; *A. bruggeni* (Gurjanova, 1938); *A. collingi* (Gurjanova, 1938); *A. ekmani* (Gurjanova, 1938); *A. georgianus*, new species; *A levidensus* (J. L. Barnard, 1956); *A. rylovi* Bulycheva, 1952; *A. tridens* (Alderman 1936); *A. villosus* Bate 1862. (*A. orientalis* Hirayama, 1986).

Diagnosis: Large atylids (10-30+ mm). Rostrum medium to large. Anterior head margin rounded, rarely bifid. Antennae moderately strongly sexually dimorphic. Antenna 1, peduncular segment 2 not longer than 1; accessory flagellum minutely 1- segmented. Antenna 2, peduncular segments 4 & 5 strong, often setose.

Lower lip, inner lobes weak or lacking. Mandible: molar triturative; palp normal, 3-segmented. Maxilla 1, inner plate with 4-8 apical setae. Maxilla 2, inner plate with 1-8 proximal plumose marginal setae. Maxilliped, palp normal, 4-segmented.

Coxae 1-4 medium deep, smooth or subacute below; coxa 3 antero-distally deepest. Coxa 5, anterior lobe broadly or sharply rounded below. Gnathopods 1 & 2 ordinary, very weakly or not sexually dimorphic; propod & carpus medium, usually subsimilar in length.

Peraeopods 3-7 not elongate, dactyls relatively short. Peraeopods 3 & 4, segment 5 markedly shorter than 4 & 6. Peraeopod 5 distinctly smaller than peraeopods 6 & 7; basis with small postero-distal lobe. Peraeopod 7, basis broad, postero-distal lobe present, rounded or acute below. Peraeopods 5-7, segment 5 markedly shorter than segments 4 & 6.

Pleopods regular; pleon plates rounded below and behind. Uropod 2 short, rami unequal. Uropod 3 strong, rami lanceolate, margins setose in male, setose and/or spinose in female.

Telson lobes not elongate, fused basally, not diverging distally. Coxal gills sac-like, weakly to moderately pleated. Brood plates medium broad, not slender.

Variables: Rostrum long (type), medium (*A. collingi, A. georgianus*); posterior peraeonites carinate (type), smooth (*A. borealis, A. rylovi, A. tridens*); pleon carinate (type), smooth (*A. borealis, A. rylovi, A. tridens*); gnathopod 2, propod & carpus short, stout (type), slender (*A. bruggeni, A. ekmani, A. villosus*); peraeopods 5-7, segment 5 only slightly shorter than segments 4 & 6 (*A. villosus*).

Taxonomic Commentary: Some species of the genus *Atylus*, as here defined, overlap in some character states, with some species of *Nototropis*, as defined below (p.28). However, the two genera are distinguished by the characters of the subfamily key (p. 8) and, in combination, by the larger rostrum, heavier mandibular palp, the weak (or lacking) hind lobe of the basis of peraeopod 5, heavier uropod 3, and the pleated, rather than phylloform (or dendritic) anterior coxal gills, especially in the male.

Distributional Commentary: Most species are confined to subarctic and boreal coastal marine waters of the North Pacific region, and are mainly benthic. *Atylus carinatus* is holarctic, but *A. villosus* has been recorded only from the southern oceans and may not be a natural member of the genus.

Members of the genus *Atylus* (sens. str.) are virtually non-overlapping distributionally with members of the genus *Nototropis*, as here defined.

KEY TO NORTH PACIFIC SPECIES OF ATYLUS*

(Character states illustrated mainly in Fig. 1, p. 6)

1. Peraeon segments 6 & 7 and pleon mid dorsally toothed or carinated; urosome segment 1 with single (or bifid) mid-dorsal tooth; coxa 4 various, not crescent shaped posteriorly . . . . . 2.
—All segments of peraeon and pleon mid-dorsally smooth; urosome segment 1 with single mid-dorsal tooth and preceding notch; coxa 4 crescent-shaped postero-ventrally . . . . . 8.

2. Rostrum large (1/2 head length); uropod 3 large, rami longer than twice peduncle, margins with spines and setae; telson lobes elongate, 1 1/2 - 2 X basal width . . . . . 3.
—Rostrum medium, 1/4-1/3 head length; uropod 3 medium, rami shorter than twice peduncle, margins spinose; telson lobes short, length ≡ width . . . . . 7.

3. Gnathopod 2, propod and carpus stout, depth of each > 1/2 length; peraeopod 7, basis, posterior lobe large, acute below; fused urosome segments 2 & 3 with low mid-dorsal carination; mandible, palp stout, segment 3 setose . . . . . 4.
—Gnathopod 2, propod and carpus slender, depth < 1/2 length; peraeopod 7, posterior lobe small, shallowly rounded below; fused urosome segments 2 & 3, dorsal process erect, projecting well above mid line . . . . . 5.

4. Peraeopods 3 & 4 & peraeopod 6, segment 5 short, length < 1/2 segment 4; gnathopod 2, propod stout, length > carpus . . . . . ***A. atlassovi*** (p. 11)
—Peraeopods 3 & 4, and peraeopod 6, segment 5 medium, length > 1/2 segment 4; gnathopod 2, propod small, length < carpus . . . . . ***A. carinatus*** (p. 11)

5. Eyes large; fused urosome 2 & 3 with bifid mid-dorsal tooth; uropod 3, margins of rami with spines and setae; peraeopod 7, basal lobe subacute . . . . . ***A. bruggeni*** (p. 14)
—Eyes small; fused urosome 2 & 3 with single mid-dorsal tooth; uropod 3 (female), ramal margins spinose; peraeopod 7, basal lobe rounded below . . . . . 6.

6. Pleon segment 3 and urosome segment 1 with bifid mid-dorsal tooth; western Pacific, Sea of Japan . . . . . ***A. ekmani*** (p. 16)
—Pleon segment 3 and urosome 1 with single mid-dorsal tooth; endemic to the North American Pacific coast . . . . . ***A. levidensus*** (p. 16)

7. Coxa 4 acute below; fused urosome 2 & 3 with low mid-dorsal ridge; gnathopod 1, propod, postero-distal angle with 5-6 transverse row of stout spines . . . . . ***A. collingi*** (p. 24)
—Coxa 4 rounded below; urosome segments 2 & 3, with erect mid-dorsal tooth; gnathopod 1, postero-dorsal, angle of propod with 3 transverse rows of spines . . . . . ***A. georgianus*** (p. 26)

8. Peraeopod 6, segment 5 short (< 1/4 segment 4); telson large, length >> width . . . . . 9.
—Peraeopod 6, segment medium (= 1/2 segment 4); telson short, basal width about equal to length . . . . . ***A. rylovi*** (p. 18)

9. Antennae long, flagella with more than 20 segments; uropod 3 (female), apices of rami acute; telson elongate, length 1.5 X width . . . . . ***A. tridens*** (p. 20)
—Antennae shorter, flagella with fewer than 20 segments; uropod 3 (female) apices of rami rounded; telson medium, length 1.3 X width . . . . . ***A. borealis*** (p. 22)

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* *Atylus orientalis* Hirayama not included

Atylus carinatus (Fabricius)
(Fig. 3)

Gammarus carinatus J. C. Fabricius, 1793: 515.
Atylus carinatus Sars, 1895: 471, pl. 166.—Stebbing, 1906: 328.—Shoemaker, 1920: 14E.—Shoemaker, 1955: 45.—Gurjanova, 1951: 679.—Dunbar, 1954: 762.—Barnard, 1975, fig. 61.—Barnard & Karaman, 1991: 262.

Material Examined: North-west Territories: Slidre fiord, Ellesmere I., Arctic Biol. Sta., FRB, Canada, July 25, 1962 - 1 male (22.0 mm) (slide mount); 1 female ov (28.0 mm) (slide mount). Many specimens in CMN Canadian arctic collections; none from immediate study region.

Diagnosis Female (25.0-30.0 mm): Body large, laterally compressed. Peraeon and pleon segments with mid-dorsal ridge, increasingly elevated as carinations on peraeon segments 5-7, pleon 1-3, and urosome segment 1. Fused urosome segments 1 and 2 with low mid-dorsal and paired dorso-lateral ridges. Head: rostrum large (> 1/2 head length);, anterior head lobe blunt, slightly emarginate. Eye small. Antenna 1, peduncular segments 1 & 2 subequal in length, setose posteriorly; accessory flagellum small, 1-segmented. Antenna 2 slightly the longer, peduncular segments heavily setose posteriorly.

Lower lip lacking inner lobes. Mandible: molar large, strong; spine row with 5-7 blades; left lacinia 5-dentate; palp normal, strong. Maxilla 1, inner plate with 7 apical setae; palp large, 2-segmented. Maxilla 2, inner plate with 1-3 stout plumose inner marginal setae. Maxilliped normal, palp strong.

Coxal plates 1-4 medium deep; coxa 1 shortest, directed anteriorly; coxa 3, lower margin anteriorly subacute. Coxa 5, anterior lobe broadly rounded. Gnathopods 1 & 2, very weakly sexually dimorphic; carpus and propod relatively short, deep, subequal in length.
Peraeopods 3 & 4, segment 5 shorter than segments 4 & 6, dactyls stout. Peraeopods 5-7 (especially bases) somewhat dissimilar in form and size; segment 5 slightly shorter than corresponding segments 4 & 6. Peraeopods 5 & 6, lower hind low very small, not produced. Peraeopod 7, basis broad, postero-distal lobe rounded.

Pleon plates 1-3 broad, hind corners squared. Uropod 1, rami lanceolate, subequal. uropod 2, outer ramus markedly shorter than inner. Uropod 3, rami narrowly lanceo-late, > 3X peduncle; margins setose in female and male.

Telson lobes deeply separated, not diverging, each with apical and subapical spines. Coxal gills large, sac-like, on peraeopods 2-7, anterior gills (male) weakly pleated basally.

Distributional Ecology: Holarctic, in North America south to the Saguenay fiord in the east, and northern Bering Sea (Kotzebue Sound) in the west (Shoemaker, 1955) mainly in shallow coastal waters (0-50 m), along mixed stony and silty shores. The species has been recorded from the stomach contents of various arctic shallow-water fishes, and from eider ducks, and bearded and ringed seals (Dunbar, 1954).

Taxonomic Commentary: *Atylus carinatus* is a distinctive species of the genus that exhibits several plesiomorphic character states. These include the accessory flagellum, strongly carinated dorsum of the posterior thoracic and abdominal segments, and the strongly marginally setose rami of uropod 3 (both sexes). As the type of the genus *Atylus*, its combination of character states separate it at genus level from *Anatylus pavlovi* Bulycheva, 1955, and from *Nototropis smitti* (Goes, 1866) with which *A. carinatus* overlaps distributionally in high arctic and subarctic waters.

Atylus atlassovi (Gurjanova)
(Fig. 4)

Nototropis atlassovi Gurjanova, 1951: 690, figs. 77A, B.
Atylus atlassovi Mills, 1961: 19 (key only).—Barnard & Karaman, 1991: 262.

Material Examined: Bering Sea region: Amchitka Island, Constantine Harbor, C. E. O'Clair coll., Oct. 5, 1969 - July 14, 1970: 4 lots with 15 specimens, including males, females, and immatures; female ov. (20 mm) (slide mount) fig'd. St. Matthew Island, Walrus Cove, P. Slattery coll., June 29, 1983.- 1 male (28.0 mm)(fig.'d) CMN collections.

Diagnosis. Female (20.0 mm): Body large compressed. Peraeon segments each with shallowlly indented mid-dorsal ridge, slightly elevated to weak carinations on segments 6 & 7. Mid-dorsal carination weak on pleon segments 1-3, strong on urosome 1, medium on fused urosome segments 2 & 3. Head: rostrum large (> 1/2 head length); anterior head lobe broad, shallowly imarginate. Eye medium, vertically ovate. Antenna 1, peduncular segment 2 not longer than 1, hind margin thickly short-setose; peduncle 3 short; accessory flagellum minute. Antenna 2, peduncular segments 4 & 5 stout, anterior and posterior margins setose.

Lower lip lacking inner lobes. Mandible: molar strong; spine row with 8-10 blades and accessory setae; left lacinia 5-dentate; palp stout, setose. Maxilla 1, inner plate with 10-12 apical setae; palp stout, 2-segmented. Maxilla 2, inner plate with several inner marginal plumose setae. Maxilliped stout, palp segment 2 short.

Coxal plates 1-4 relatively broad , lower margins nearly straight; coxa 1 about as deep as 2, weakly directed forward. Coxa 5, anterior lobe acute below. Gnathopods 1 & 2 stout, 2 larger, moderately sexually dimorphic; propods relatively large, deep; carpus deep, shorter than respective propod. Gnathopod 1, propod with single distal row of pectinate setae; posterodistal angle with 3 rows (4-5 in male) of stout clasping spines. Gnathopod 2, propod, postero-distal angle with 2 rows (3 in male) of stout spines.

Peraeopods 3 & 4 stout, margins spinose; segment 5 small, much shorter than segments 4 & 6; dactyls short. Peraeopods 5-7, not markedly dissimilar; segment 5 much

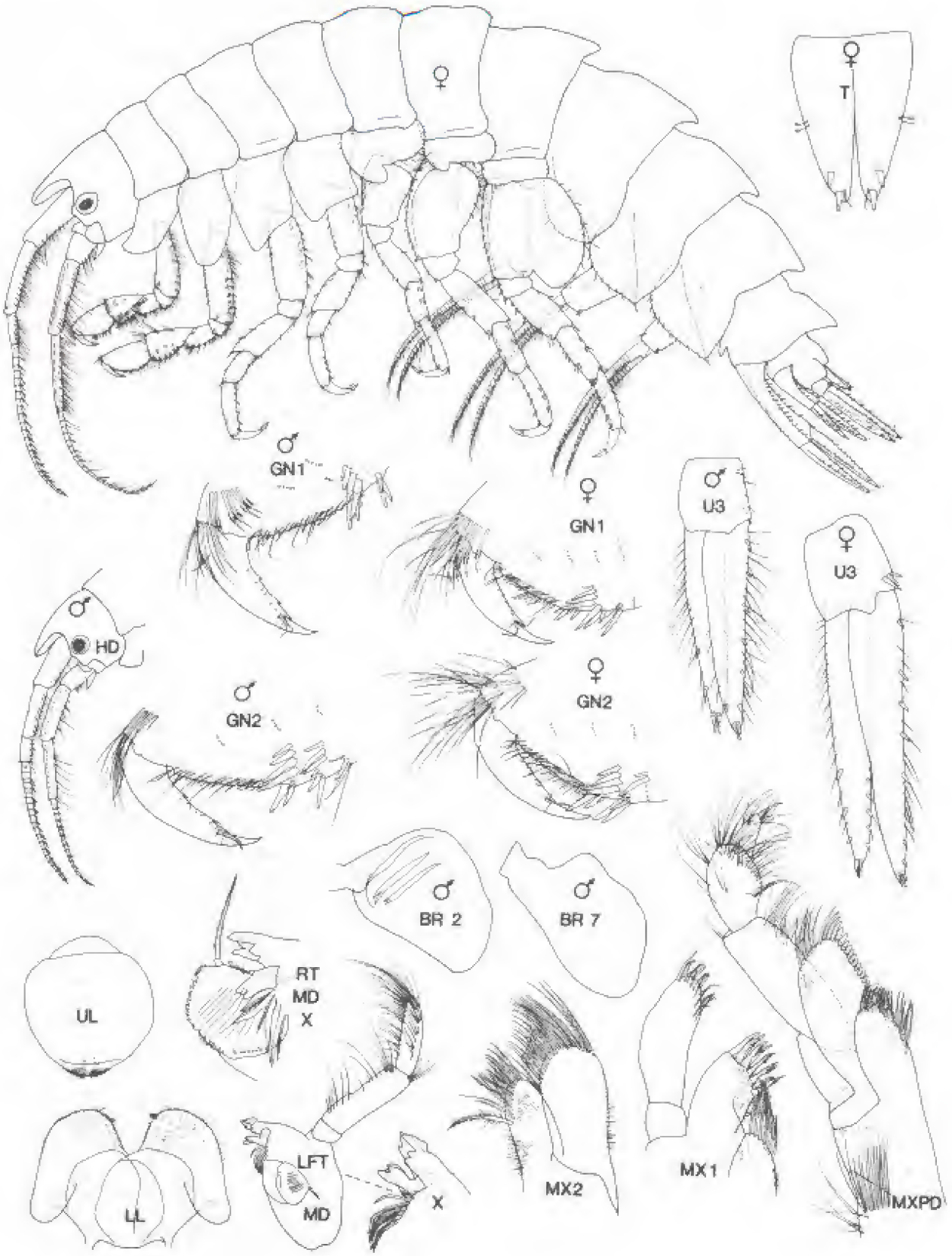

FIG. 3. ***Atylus carinatus*** **(Fabr.). Female (28.0 mm), Male (22.0 mm) Slidre Fiord, Ellesmere I.**

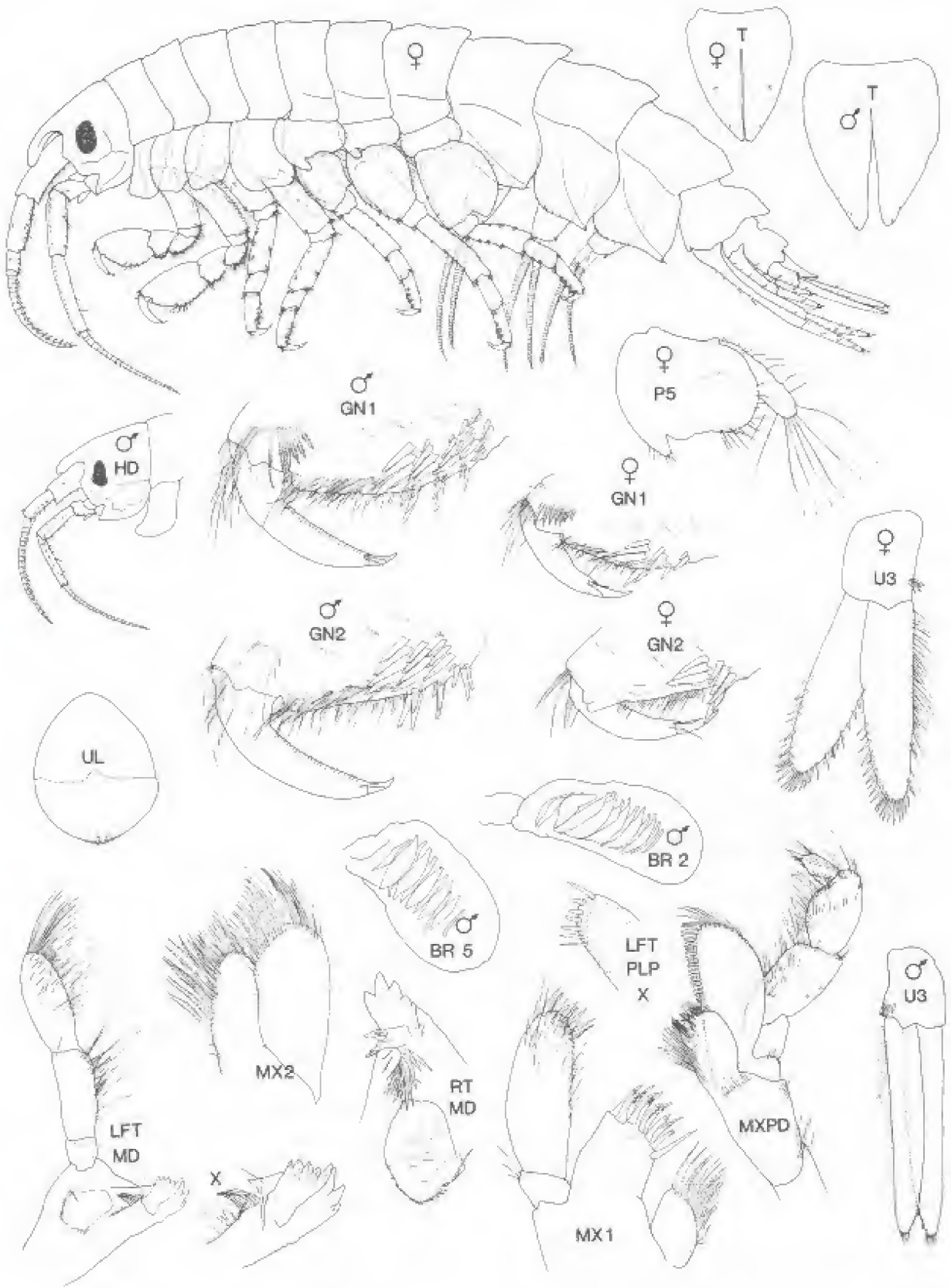

FIG. 4. *Atylus atlassovi* **(Gurjanova). Female br. III (20.0 mm) Constantine Harbor, Amchitka I. Male ((27.0 mm). St. Matthew I., Bering Sea.**

shorter than segments 4 & 6; peraeopod 5, basis with weak lower hind cusp. Peraeopod 7, basis broad, lower hind lobe acute.

Pleon plates 1-3 broad, hind corners acuminate. Uropod 3, rami large, broadly lanceolate, margins bluntly rounded and spinose apically (female); rami larger, nar-rowly lanceolate, inner margins setose and spinose.

Telson lobes, medium, fused basally, narrowing distally, apices nearly bare.

Coxal gills sac-like, moderately pleated in males, on peraeon segments 2-7.

Distributional Ecology: Sea of Okhotsk (Kamchatka peninsula) to Bering Sea and Sea of Okhotsk, in subtidal shallows.

Taxonomic commentary: *Atylus atlassovi* is a distinctive but relatively primitive species. It clusters most closely with*A. carinatus*, at less than 75% similarity level (p. 60).

Atylus bruggeni (Gurjanova)
(Fig. 5).

Nototropis bruggeni Gurjanova, 1938: 325, figs. 36, 37.—Gurjanova, 1951: 680, fig. 475.
Atylus bruggeni Mills, 1961:(key only).—Barnard & Karaman, 1991: 263.

Material Examined:
BERING SEA; St. Lawrence I., P. Slattery coll., July 10, 1980 - 1 male 1 female. Ibid, June, 1983 - 1 male, 1 female (br. I), 10 im. Panuk I,gravel, 5 m., P. Slattery coll., June 6, 1983, 3 lots - male (14.5 mm) (slide mt.); female br. II (16.0 mm) (slide mt.); 200+ specimens including many males and some females ov.

St, Matthew I., Walrus Cove, P. Slattery, June 27/83 - 3 lots (8 spms). Ibid, Big Bite Bay, June 15/86 - male (15.0 mm (slide mt.); female ,with young (19.0 mm) +40 other specimens, including mature males, females with brood young.

Pribilof I., St. Paul I., D. B. Quayle coll. Nov. 21, 1965 - 11 specimens.
ALASKA MAINLAND: Off Icy Cape, 2 ft. in depth, P. Slattery coll., June 24, 1984 - 4 specimens. Off Wainwright, June 22/84 - 11 specimens.
ALEUTIAN ISLANDS: Amchitka I., Constantine Harbor, C. E. O'Clair coll. April 26, 1969 - 1 male (22.0 mm) (slide mount). Ibid, Sept. 27, 1969 - 1 male, 1 female. CMN collections.

Diagnosis: Male (15.0mm), female (10.0 mm): Body large, strongly compressed., Peraeon and pleon with mid-dorsal ridge, elevated to medium strong carina on peraeon segments 6 & 7, and pleon segments 1-3. Urosome segments 1, and fused 2 & 3, each with bifid mid-dorsal carina, posterior tooth much the stronger. Head: rostrum large (>> 1/2 head length); anterior head lobe shallow, excised below eye. Eyes large, oval, larger in male. Antennae slender. Antenna 1 relatively short, peduncular segment 2 shorter than 1 (female), subequal (male), margins weakly setose (brush setae in male); segment 3 short, accessory flagellum minute. Antenna 2, peduncular segment 5 much longer than 4, margins sparsely setose; segments 3 & 4 with brush setae (male).

Lower lip lacking inner lobes. Mandible: molar strong; spine row with 5 blades and accessory setae; left lacinia 4(5) dentate; palp slender, weakly setose. Maxilla 1, inner plate with 8 apical setae; palp stout. Maxilla 2, inner plate with several inner marginal pectinate setae. Maxilliped, palp slender, dactyl long.

Coxae 1-4 medium, lower margins various; coxa 3, anteriorly subacute below. Coxa 5, anterior lobe small subacute. Gnathopod 1 & 2 slender, very slightly sexually dimorphic, somewhat dissimilar, 2 the larger. Gnathopod 1, propod and carpus small, short; propod with antero-distal row of about 15-20 pectinate setae, and 3 clusters (2 in female) of longish spines at the postero-distal angle. Gnathopod 2, propod and carpus more slender and longer; basis, margins lined with long setae.

Peraeopods 3 & 4 medium strong; segment 5 small, much shorter than segments 4 & 6; dactyls short. Peraeopods 5-7 rather dissimilar in form; segment 5 shorter than segment 6 and much shorter than 4. Peraeopods 5 & 6, bases lacking postero-distal lobes. Peraeopod 7, basis broad, subacutely produced below.

Pleopods strong. Pleon plates 1-3 broad, hind corners acuminate. Uropods 1 & 2 strong, rami unequal. Uropod 3, rami lanceolate, margins setose (male), spinose and very weakly setose (female).

Telson ordinary, lobes fused basally, not diverging distally; apices each with single small spine.

Coxal gills large, sac-like, simple (female); anterior gills moderately pleated (male)

Distributional-Ecology: Bering Sea to Sea of Japan, in depths of 10 - 80 metres, mainly on sand. In North America, from St. Lawrence Island and the Pribilof Islands to the Aleutian chain and mainland Alaska, from the shore line to depths of more than 10 m.

Taxonomic commentary: This species is distinguished by its large body size and low body carinations, except on the urosome where it is bicuspate on fused urosome segments 2-3. Among other distinguishing features, the gnathopods and uropod 3 (esp. in the male) are very setose, and the mandibular palp is slender. This species evinces plesiomorphic character states such as the weakly subchelate and long wristed gnathopods (both sexes) and strongly rostrate head. It also possesses apomorphic features such as the weakly 5-dentate mandibular left lacinia and weakly pleated coxal gills.

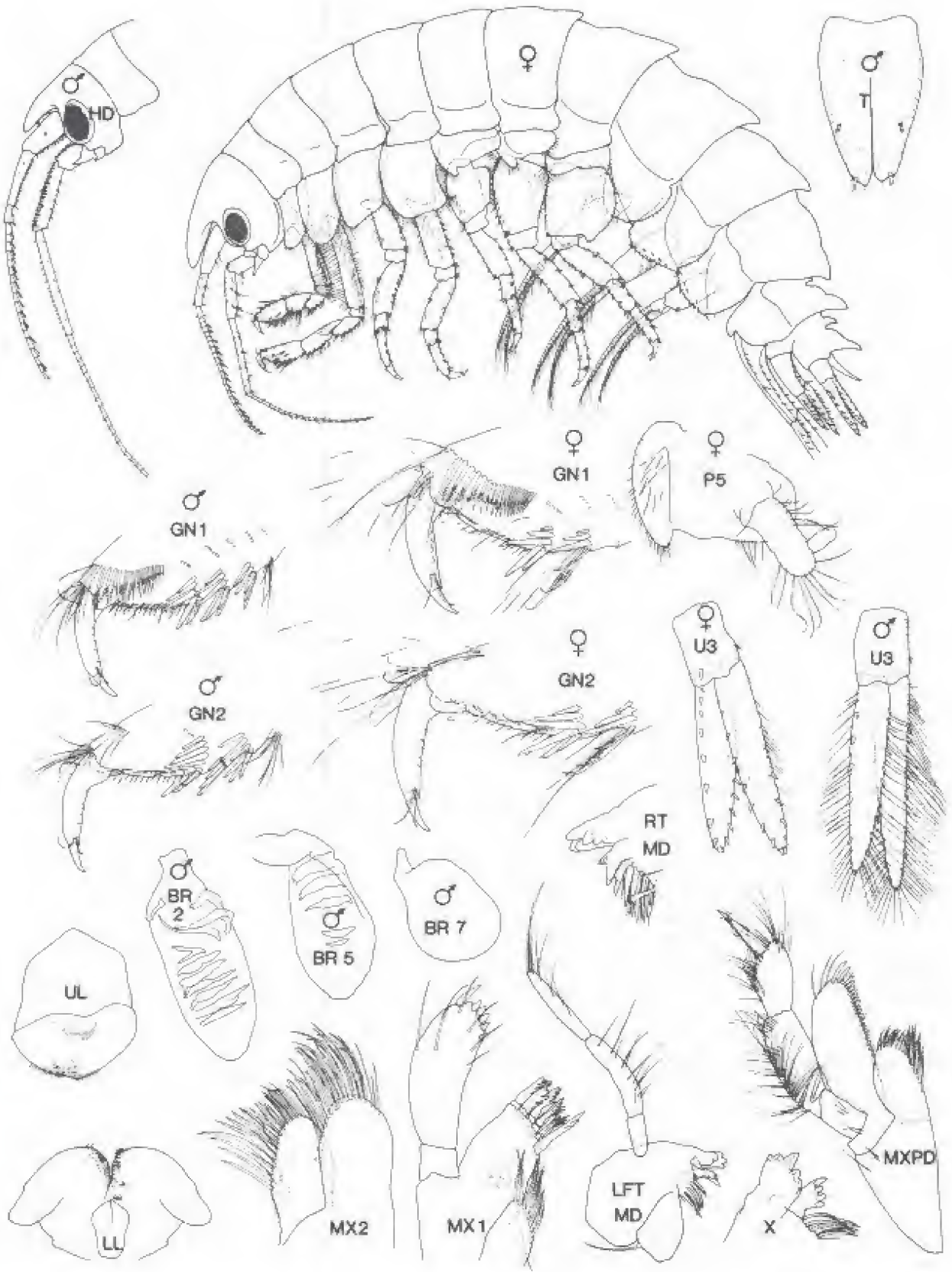

FIG. 5. ***Atylus bruggeni*** **(Gurjanova). St. Matthew I., Bering Sea. Female ov (19.0 mm) Male (15.0 mm).**

Atylus ekmani (Gurjanova)
(Fig. 6)

Nototropis ekmani Gurjanova, 1938: 323, fig. 35.—Gurjanova, 1951: 685, fig. 473.—Tzvetkova, 1968: 172.
Atylus ekmani Mills, 1961: 19 (key).—Barnard & Karaman, 1991: 264 (list).—Okado, 1993: 7.

Diagnosis. Female (20 mm): Body large strongly compressed laterally. Peraeon and pleon with mid-dorsal ridge elevated to low carinae posteriorly on peraeonal segments (5) 6-7, and pleon segments 1-2. Pleosome segment 3 and urosome segment 1, each with strong bifid mid-dorsal tooth. Fused urosome segments 2 & 3 with single acute mid-dorsal carina. Head: rostrum arched, medium to large (~ 1/2 head length); anterior head lobe narrow, angles rounded. Eyes small to medium, subovate. Antennae slender, not elongate. Antenna 1, peduncular segment 2 shorter than 1, weakly setose behind; segment 3 short; accessory flagellum vestigial. Antenna 2, peduncular segments 4 & 5 weakly setose.

Lower lip not described (inner lobes probably lacking). Mandible: molar strong; spine row with 6-7 narrow blades and accessory setae; left lacinia 5 1/2 dentate; right lacinia bifid, tips flabellate; palp slender, weakly setose. Maxilla 1, inner plate with about 6 apical setae; palp strong. Maxilla 2, inner margin of inner plate with single stout plumose seta. Maxilliped, plates large, palp slender slightly shortened.

Coxal plates 1-4 narrow, shallow, subacute below; coxa 5, anterior lobe small, sharply rounded. Gnathopods 1 & 2 small, slender, unequal, little or not sexually dimorphic, bases not strongly setose behind. Gnathopod 1, carpus medium depth, as long as propod; propod, inner face anteriorly with 5-6 rows of pectinate setae, distal 2 rows each with more than 20 setae. Gnathopod 2, carpus slender, longer than propod.

Peraeopods 3 & 4 strong, spinose; segment 5 distinctly shorter than segments 4 & 6; dactyls medium. Peraeopods 5-7 dissimilar, segment 5 shorter than segment 6 and very much shorter than elongate segment 4. Peraeopods 5 & 6, bases with very small acute postero-distal lobes. Peraeopod 7 moderately broad, postero-distal lobe small, rounded below.

Pleopods undescribed. Pleon segments medium broad, hind corners mucronate. Uropods 1 & 2 stout, rami unequal, margins spinose. Uropod 3, rami subequal, lanceolate, ~ 2X length of peduncle, margins spinose.

Telson lobes long, narrow, fused in basal 1/4, apices not diverging, each with notch and small spine. Coxal gills not described.

Distribution: Western North Pacific: Russian coast of the Japan Sea and southern Hokkaido, north to the Okhotsk and western coast of the Bering Sea, at subtidal depths.

Taxonomic Commentary: Mills' key to species of *Atylus* includes *A. ekmani* erroneously in the group with 2 dorsal teeth on urosome 5 & 6. This oversight, pointed out by Okada (1993), is corrected in the present key (p. 10). The species clusters most closely with *P. bruggeni* and *P. levidensus* (p. 60). Features in common include the very thin body, carinated abdomen, weak gnathopods (propod of gnathopod 1 with heavy pectinate setae), unevenly scalloped lower margins of the anterior coxal plates, and the short, spinose uropod rami in both sexes.

Atylus levidensus J. L. Barnard
(Fig. 7)

Atylus levidensus J. L. Barnard, 1956: 38, pls. 13, 14.—Mills, 1961: 19, fig. 1.—Barnard, 1969b: 94.—Barnard, 1975: 340, 359, fig. 133.—Austin, 1985: 604.—Staude, 1987: 382.—Barnard & Karaman, 1991: 264.

Material Examined (CMN collections, Ottawa):
S. E. ALASKA: Prince William Sound (Kayak I.) through outer coast (Sitka region), to southern Alexander Archipelago (Bronson Bay), ELB Stns, June-Aug., 1961 - 51 specimens in 8 lots, at: A3(1), A6(1), A22(11 - [including female br III (10.5 mm) (slide mt.), male (7.0 mm) (slide mt.)], A75(7), A80(5), A112(1), A151(5), A175 (20). ELB Stns., Lisianski Strait to Sitka region, 1980 - 8 specimens in 5 lots at: S4B3(1), S4B4(1), S8B1(2), S11B2(1), S19B1(3).
BRITISH COLUMBIA:
Queen Charlotte Islands: Graham I., north, outer, and inner coasts + Masset Inlet, ELB Stns, July-Aug., 1957 - ~100 specimens in 13 lots (reported upon by Mills, 1961).
B. C. Mainland coast: Prince Rupert to Calvert Island, ELB Stns, July, 1964 - ~200 specimens in 15 lots, at: H1(19), H5(3), H7(50), H8(14), H12(16), H26(1), H33(1), H35(4), H39(50), H44(9), H47(6), H49(3), H50(10), H53(3), H65 (6).
North end Vancouver I., Cape Scott to Wickaninnish Bay, ELB Stns, July, 1959 - ~ 30 specimens in 6 lots (reported upon by Mills, 1961).
South end Vancouver I., outer coast south to Victoria, surf coast locations,in *Phyllospadix* corms; July, 1955 - 7 specimens in 4 lots (reported upon by Mills, 1961).
Barkley Sound south to Sooke, ELB Stns, 1964-77 - 80 specimens in 17 lots, at: P702(2), P719(5), P710(5), P711(1), P714(2); B3(52) [including female ov (10.5 mm) (slide mt.), male (8.5 mm) (slide mt.)], B4(5), B5(3); B8(1), B19(18).
Strait of Georgia, English Bay, ELB coll. - 1 female ov (12.0 mm) (slide mt.); 1 male (10.0 mm) (slide mt.).
WASHINGTON, OREGON: ELB Stns., Strait of Juan de Fuca to Otter Rock, July-August, 1966 - ~250 specimens in 7 lots, at: W30 (2), W34(13), W36 (62), W40(50), W42(6), W58(65), W60(48).
Coos Bay, Oregon, to Mendocino Co., CA, KE Conlan Stns, July, 1986 - ~50 specimens in 5 lots, incuding 1 female br. III (10.0 mm) (slide mt.); 1 male (7.0 mm) (slide mt.).

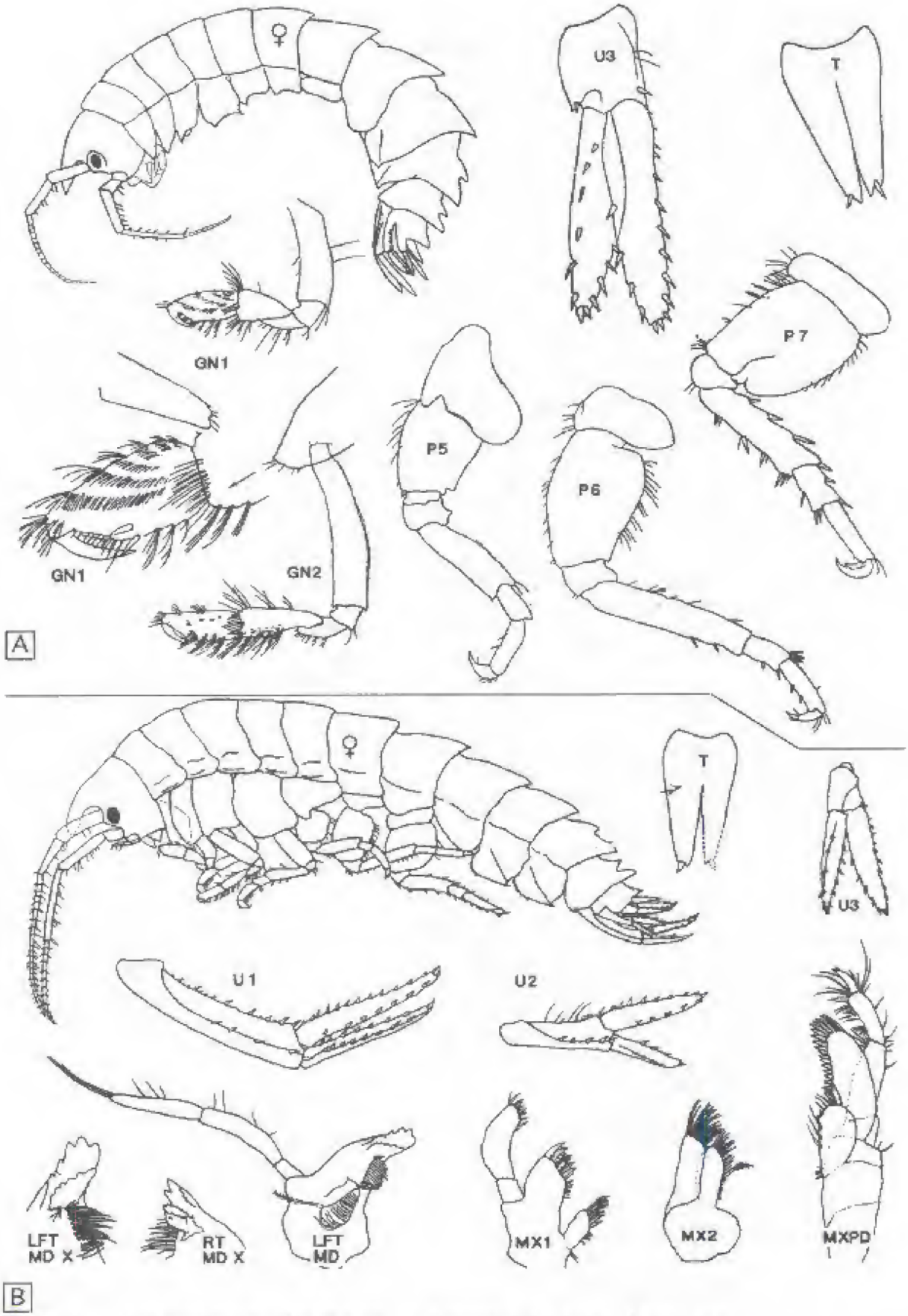

FIG. 6. *Atylus ekmani* Gurjanova **A. Female (20.0 mm). Japan Sea. (modified from Gurjanova, 1951) B. Female (20.0 mm) (modified from Okada, 1993).**

Diagnosis. Female (12.0 mm); male (7-8 mm): Body medium, strongly compressed laterally. Peraeon and pleon with mid-dorsal ridge, elevated to low carina on peraeon segment 6 & 7 and pleon segments 1-3. Urosome segments 1, and fused segments 2 & 3, each with acute elevated dorsal tooth. Head: rostrum large (~1/2 head length); anterior head lobe shallow, slightly emarginate. Eye small, oval. Antennae slender. Antenna 1, peduncular segment 2 shorter than 1, not setose behind; accessory flagellum minute. Antenna 2, peduncular segments weakly setose.

Lower lip lacking inner lobes. Mandible: molar strong; spine row with 4-5 blades and accessory setae; left lacinia 4 1/2 - dentate; palp slender, weakly setose. Maxilla 1, inner plate with 5 apical setae, palp strong. Maxilla 2, inner plate with single large inner marginal plumose seta. Maxilliped, palp slender, inner plate relatively short.

Coxal plates 1-4 medium, little overlapping basally; coxa 1 not directed forward; coxa 3 anteriorly acute below. Coxa 5, anterior lobe narrowly acute below. Gnathopods 1 & 2 not discernibly sexually dimorphic; propod short, small, with distal row of numerous pectinate setae; carpus slender, little longer than propod.

Peraeopods 3 & 4 relatively short; segment 5 small, much shorter than segments 4 & 6; dactyls short. Peraeopods 5-7 somewhat dissimilar in size and form; segment 5 small, shorter than segment 6 and much shorter than segment 4; bases moderately expanded, lower hind lobes very small, not produced.

Pleopods relatively short, weak. Pleon plates 1-3 medium broad, hind corners obtuse. Uropods 1 & 2 relatively short, outer ramus the shorter. Uropod 3, rami short (~ 2X peduncle), thick, margins spinose (both sexes).

Telson lobes narrow, slightly diverging distally, apices with single stout spine. Coxal gills on peraeopods 2-7, medium large, weakly pleated in male.

Distributional Ecology. North American Pacific: from Prince William Sound (S.E. Alaska) southward through British Columbia to Central California (rare south of Monterrey) along open, high salinity, surf-exposed, bedrock shores, frequently among corms of *Phyllospadix*, in the lower intertidal zone. It was not taken in dredge hauls and is therefore ranked as a truly littoral zone species. It was also seldom collected in the summer-warm, relatively brackish shallows of the Strait of Georgia.

A. levidensus, and A. tridens, were the only two species of *Atylus* collected in modest abundance.

Taxonomic Commentary: The species shows little variation in body size or morphology throughout its range, but is endemic to cold-temperate waters of the North American Pacific coast. It clusters above the 75% similarity level with *A. ekmani* of western Pacific shores but only at the 65% level with *A. bruggeni* of the intervening Bering Sea region (Fig. 30, p. 60).

Atylus rylovi (Bulycheva)
(Fig. 8)

Nototropis rylovi Bulycheva, 1952: 221, fig. 21.
Atylus rylovi Barnard & Karaman, 1991: 264. Ishimaru, 1994: 42.

Diagnosis. Female ov. (11.0 mm): Body medium, compressed. Peraeon segments dorsally smooth. Pleon segments 1-3 with low mid-dorsal ridge that becomes a weak carina posteriorly. Urosome 1 with posterior mid-dorsal carination and pre-ceding notch. Fused urosome segments 2 & 3 with raised mid-dorsal tooth. Head: rost-rum arched medium-large (@ 1/2 head length); anterior head lobe notched medially. Eyes medium, reniform. Antenna medium. Antenna 1, peduncular segment 2 not longer than 1 but ~3 X segment 3; accessory flagellum vestigial? Antenna 2, peduncular segments 4 & 5 strong, moderately setose.

Lower lip lacking inner lobes. Mandible: molar strong; spine row with 4-5 blades(?); lacinia not described; palp medium, apically setose. Maxilla 1 inner plate with 3 apical setae; palp broad. Maxilla 2, inner plate, inner marginal setae not des-cribed (several?). Maxilliped ordinary, plates and palp strong.

Coxal plates 1-4 medium large, hind margins setose, lower margins gently convex. Coxa 5, anterior lobe broadly rounded below. Gnathopods 1 & 2 medium slender, 2 the larger; margins of bases not strongly setose. Gnathopod 1, carpus not elongate, slightly shorter than propod; distal pectinate setae of propod not described. Gnathopod 2, propod and carpus longer and more slender than in gnathopod 1.

Peraeopods 3 & 4, segment 5 small, much shorter than segments 4 & 6; dactyls short. Peraeopods 5-7 not markedly differing in length; segment 5 shorter than 6 and much shorter than segment 4 (especially in peraeopod 6); dactyls short. Peraeopods 5 & 6, hind lobes small, not produced below. Peraeopod 7, hind lobe of basis sharply rounded below.

Pleon plates 1-3 broad, hind corners obtuse. Uropods 1 & 2 not clearly shown or described. Uropod 3, rami short (~ 2X length of peduncle), broadly lanceolate, margins spinose. Telson short (width 3/4 length), lobes short, fused basally, apices narrowing abruptly, each with 1-2 short spines. Coxal gills and brood plates not described.

Distributional Ecology: Peter-the-Great Bay, Russian coast of the Sea of Japan, in the littoral zone. Ovigerous females in September.

Material of this species was not obtained at North American Pacific stations.

Taxonomic Commentary: Although originally assigned to the genus *Nototropis* (Bulycheva, loc. cit.), *rylovi* is clearly referable to the genus *Atylus* in the form of its antennae, peraeopods, uropods and telson. *Atylus rylovi* clusters with the *A. tridens* group, including *A. borealis*.

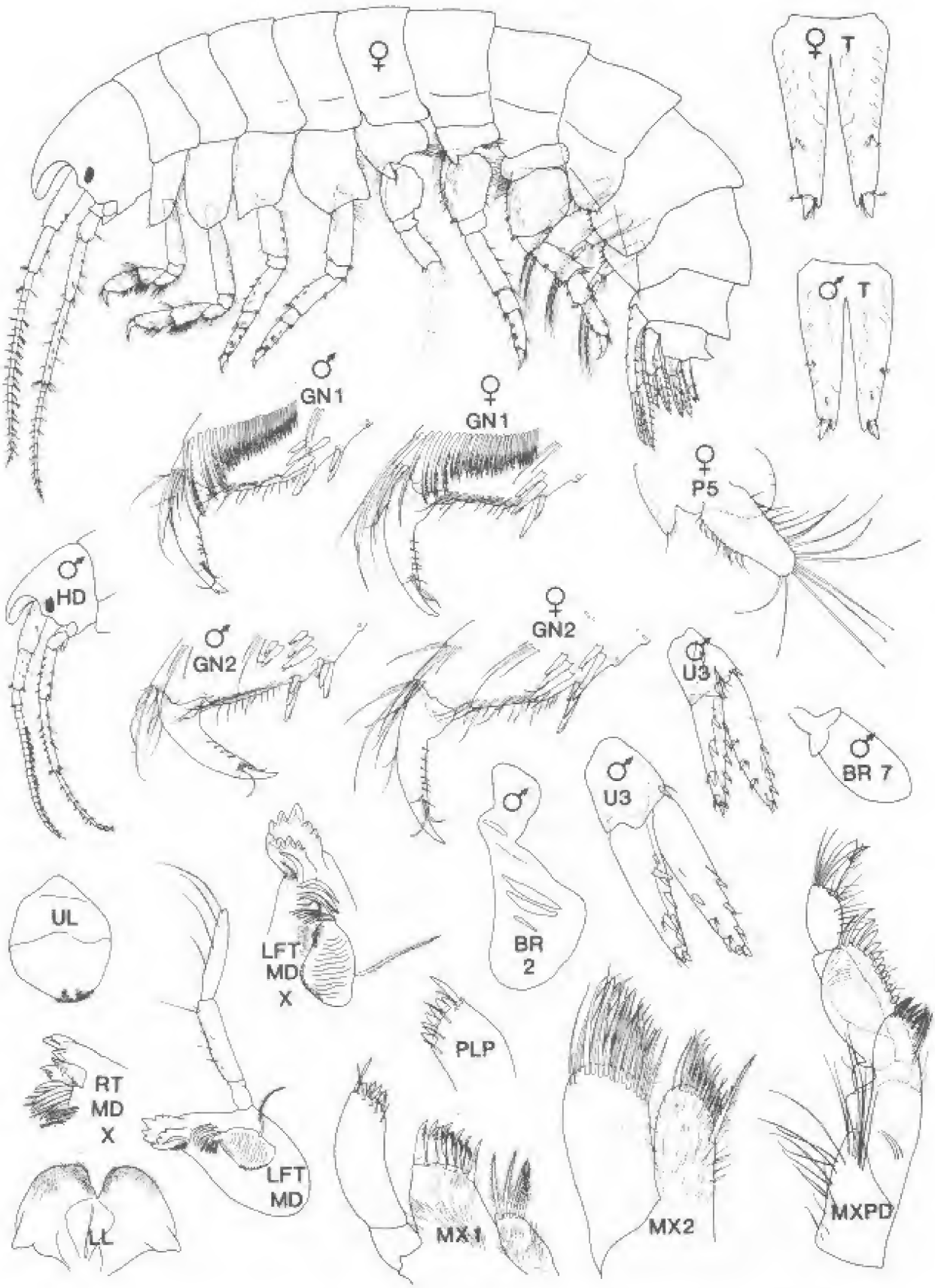

FIG. 7. ***Atylus levidensus*** **Barnard. English Bay, B. C. Female ov (12.0 mm) Male (10.0 mm)**

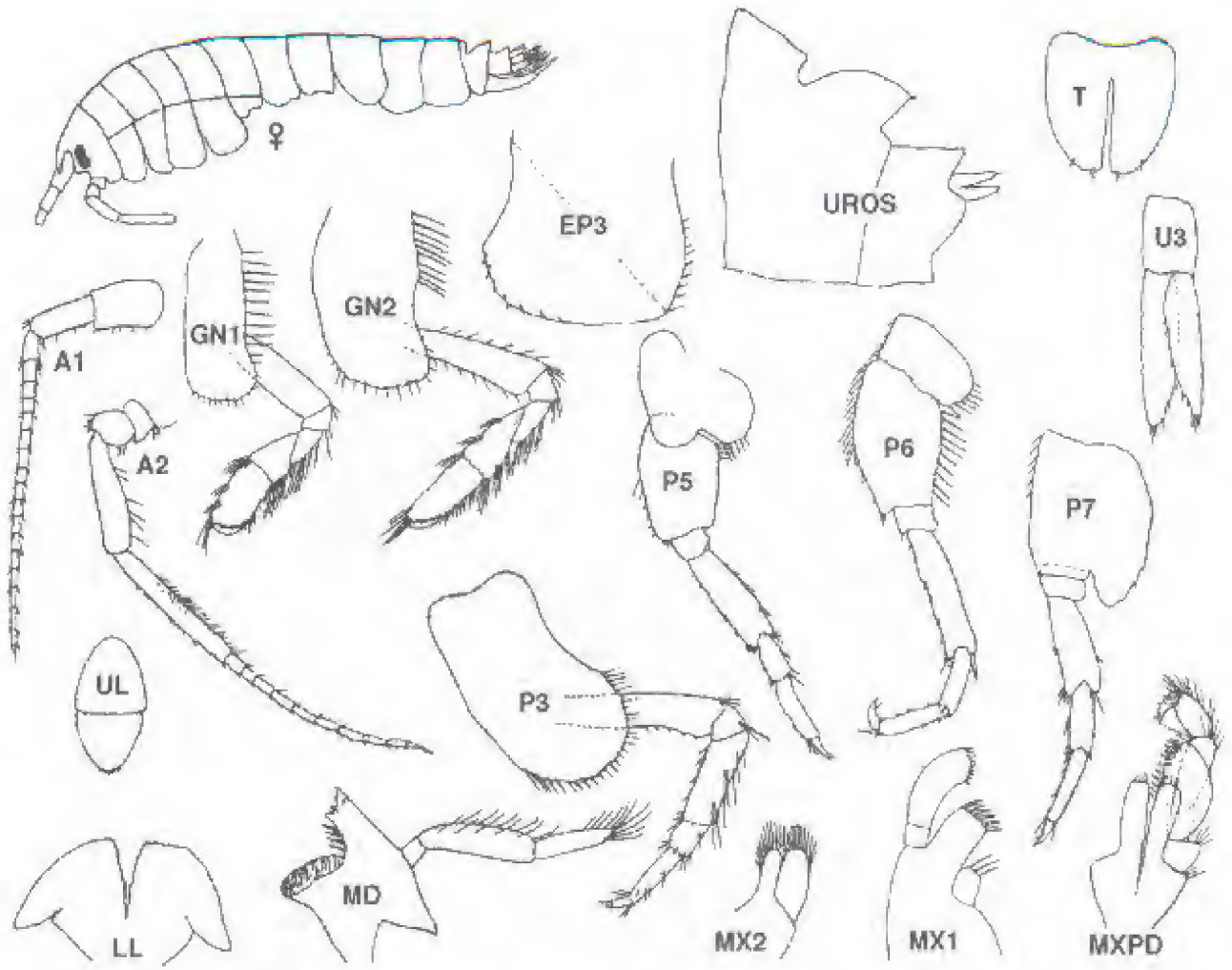

FIG. 8. ***Atylus rylovi*** **Bulycheva, 1952. Female ov. (11.0 mm). Japan Sea. (modified from Bulycheva, 1952)**

Atylus tridens (Alderman)
(Fig. 9)

Nototropis tridens Alderman, 1936: 58, figs 20-25.
Atylus tridens Mills, 1961: 25, fig. 3 (partim- non-pelagic stage).—Barnard, 1975: 346, 359, fig. 216. —Austin, 1985: 604.—Staude, 1987: 382, figs. 18.54, 18.63.—Barnard & Karaman, 1991: 265.

Material Examined (CMN collections, Ottawa):
SE ALASKA: None clearly separable from *A. borealis* in material taken at ELB Stns in 1961 or 1980.
BRITISH COLUMBIA: [Mills (1961) reported on 1955-59 collns].
Queen Charlotte Islands, mostly Graham I. ELB Stns, July-Aug., 1957 - 20 specimens in 6 lots, at: W2(1), W8(3), W9(9), W11(5), W12(1) E17-18(1).
B. C. Mainland, Prince Rupert ot Rivers Inlet, ELB Stns, July, 1964 - ~240 spms. in 11 lots, at: H1(3), H4(5), H7(15), H23(~80), H41(~85), H48(1), H49(2), H50(27), H52(2), H57(~30), H61(1).
S. end Vancouver I. Wickanninish Bay and Barkley Sd. to Victoria and Nanaimo. ELB Stns, July-Aug., 1970-1977 - ~200 specimens in 10 lots, at: P703 (1 male (11.5 mm) slide mt.), P713(1), P716(~50), P717(47), P719(2); B4(13), B5(2), B9(2); B5(31), B11a(~50 - incl. 1 male (11.0 mm)(slide mt.), 1 fem. ov (10.0 mm (slide mt).
WASHINGTON, OREGON: Agate Beach, and Cape Flattery to Neskowin Beach, ELB Stns, July-Aug., 1966 - ~400 specimens, mostly immatures, in 17 lots at: W33 (~200), W34(54), W36(20), W39 (8), W40 (72), W42(11+), W46 (2), W50(1), W57 (24), W61 (5).

Diagnosis: Female (10.0 mm), Male (9.0 mm) : Body small to medium, not excep-tionally compressed. Peraeon and pleon lacking dorsal carination. Urosome segment 1, and fused segments 2 & 3, each with medium tooth preceded by notch. Head: rostrum slender, medium (< 1/2 head length); anterior head lobe broad, slightly emarginate. Eyes very large, broad, subreniform (both sexes). Antennae long, medium strong. Antenna 1, peduncular segment 1 longer

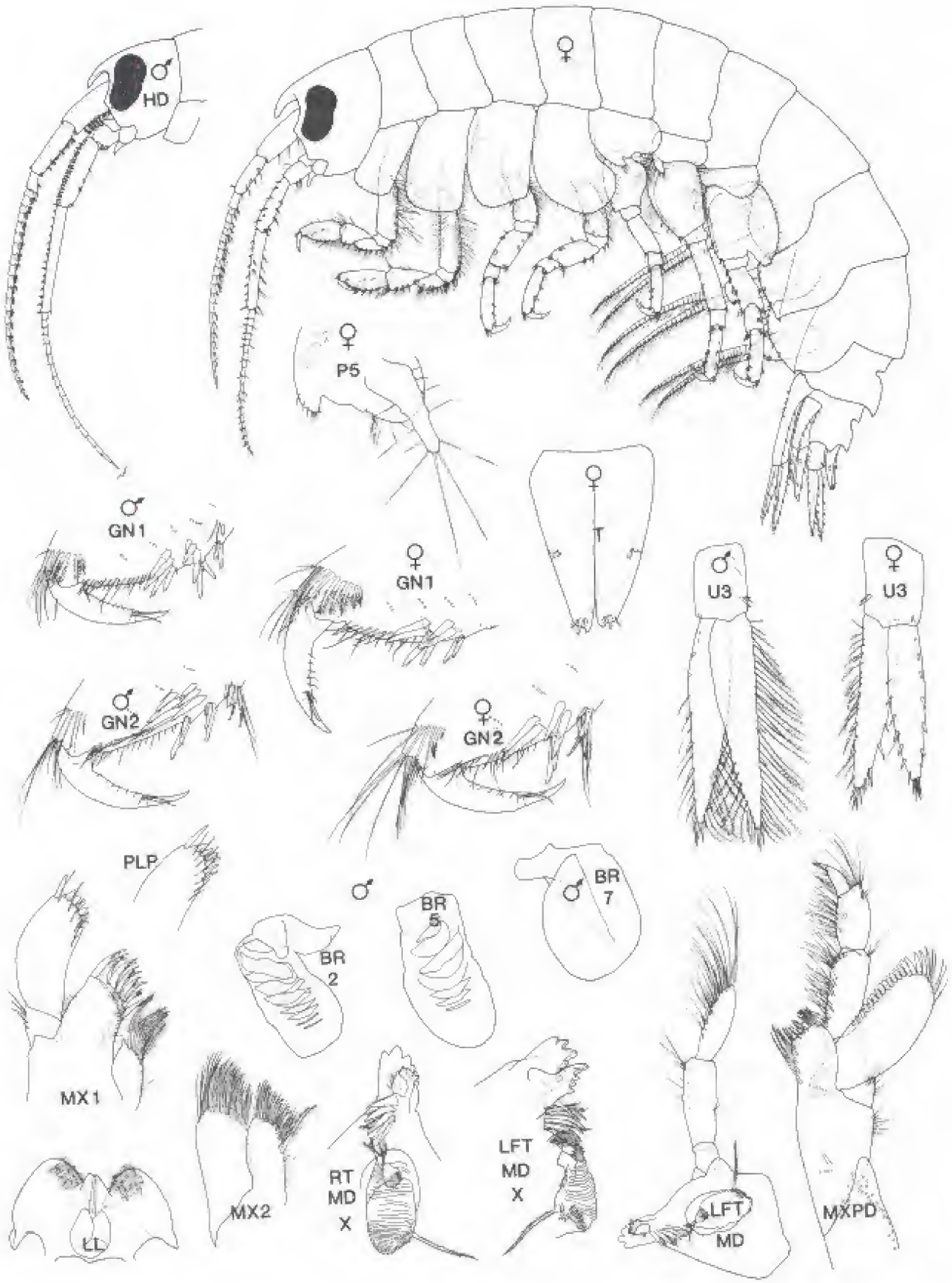

FIG. 9. ***Atylus tridens*** **(Alderman) Wickanninish Bay, B. C. Fem. (10.0 mm) Male (11.0 mm).**

than segment 2 (subequal in male, with posterior marginal brush setae); segment 3 short; accessory flagellum minute. Antenna 2, peduncular segments 4 & 5 long, moderately setose, much longer and armed anteriorly with brush setae in male; flagellum (female) with about 20 segments, each with short posterior spine.

Lower lip with weak inner lobes. Mandible: molar strong; spine row with 5-6 large blades and accessory setae; left lacinia 5-dentate, right lacinia bifid, tips flabellate; palp medium, distal segment setose. Maxilla 1, inner plate with 5 apical setae; palp broad, strong. Maxilla 2, inner plate with single inner marginal plumose seta. Maxilliped ordinary.

Coxae 1-4 broad, deep, lower margins variously convex; coxa 1 smallest, 4 largest and broadest. Coxa 5, anterior lobe small, subacute. Gnathopods 1 & 2 not grossly differing in size but moderately sexually dimorphic; bases lined posteriorly with numerous long simple setae; propod and carpus slender, not elongate; propod of gnathopod 1 armed antero-distally with 3-7 pectinate setae; postero-distal angle with 2-3 groups of spines.

Peraeopods 3 & 4 stout; segment 5 small, much shorter than segments 4 & 6 (in male, all armed posteriorly with plumose "swimming setae"); dactyls short. Peraeopods 5-7 dissimilar in size and form; segment 5 small, much shorter than segments 4 & 6. Peraeopods 5 & 6, basis moderately broadened, lower hind lobes small, unproduced. Peraeopod 7, basis broad, hind lobe acute below, with notch.

Pleopods strong, peduncles large. Pleon plates 1-3 broad, hind corners acuminate. Uropods 1 & 2 stout, rami unequal. Uropod 3, rami strongly lanceolate, margins setose (male) spinose and weakly setose (female), apex with 3 stout setae.

Telson ordinary; lobes not diverging, apices with small spine; in male, lobes more elongate and apices each armed with 3 strong setae. Coxal gills pleated, basally lobate (male).

Distributional Ecology: Queen Charlotte Islands south along outer coasts of British Columbia (few inner) to Oregon and central California, in high salinities (mostly above 29‰) in surf exposed situations, mainly in or above sand. Range extends south of *A. borealis*, although the latter was not taken S. of Juan de Fuca. Neither species was taken as far north as Prince William Sound.

Taxonomic Commentary: The material examined by Mills (1961) has been re-examined and found to consist of two distinct species of which the large "pelagic stage" is the mature form of *A. borealis*. It tends to occur in deeper, colder, upwelling areas, from Juan de Fuca north to SE Alaska.

In mature male specimens, the proximal flagellar segments were each armed poosteriorly with what appeared to be calyx-like protozoa, superficially resembling calceoli.

Atylus tridens is more abundant at southerly locations, and in summer warm, brackish waters of the Strait of Georgia.

Atylus borealis, new species
(Fig. 10)

Atylus tridens Mills, 1961: 29 & Table 2 (pelagic stage).—Barnard & Karaman, 1991: 265 (part)?

Material Examined (CMN collections, Ottawa):
SOUTHEASTERN ALASKA: ELB Stns.1961: A16, MacArthur Bay, Kuiu I. June 6 - 1 male (17 mm), 9 imm.; A59, Dixon Hbr., greenling stomach contents, June 19 - 1 subadult male; A140, McLeod Harbor, Montague I., June 13 - 4 males 1 female, 1 im.
Chichagof I. to Kruzof I., ELB Stns, 1980: - ~75 specimens in 8 lots at: S4B2(1), S4B3(1), S4B4(~40), S4B5(2), S4B6(1), S11B3(25), S18B1(2), S19B1(3 - incl. 1 female (br. III)}.
BRITISH COLUMBIA:
Queen Charlotte Islands, Graham I., ELB Stns, 1957: H14, Yakan Pt., Aug. 25 - Male (20.0 mm) Holotype, CMN Cat. No. NMCC1994-0384; 1 female (13.0 mm) Allotype, CMN Cat. No. NMCC 1994-0385; many paratypes, mostly juveniles, but including 4 males (to 17 mm), and 12 females, CMN Cat. No. NMCC1994-0386; H13 (Skonun R. mouth) - 1 male (subad); H11 (1/2 m. south of Old Masset), Aug. 27 - 1 male, 1 imm.
Mainland coast, ELB Stns, 1964: H10, Oval Bay, SW end, July 12, 1964 - 1 male, 5 females ov (slide mts.).
Vancouver Island, ELB Stn V4, Roller Bay, July 22, 1959 - 1 female, 3 imm; P703, McKenzie Beach, July 7, 1970 - 1 male 1 female (with young); Pachena Bay, P. Slattery coll., from whale pits, April 15, 1982 - 6 males, 10 fem. (ov, Br. III), 8 imm; ELB Stn P708, July 17,1970 - 1 male.
[Note: Mills listed to following material from B. C.(pelagic form): Sta F6 (Telegraph Cove, Victoria) - 2 pelagic males, 1 female ov (18.0 mm) (slide mt.); Sta. F8 (Garrison Bay, below) - 8 pelagic males (among eel grass, as below); Sta. H14 (Yakan Pt., QCI) - 5 males (as above)].
WASHINGTON: San Juan I., Stn F8, Garrison Bay, in eel grass, ELB collns., July 21, 1955 - 8 males (14-20 mm), 1 female (br. III) (slide mts.).

Diagnosis: Male (17.0 mm), Female (13.0 mm?): Body large, not exceptionally compressed. Peraeon lacking dorsal ridge or carination. Pleon with very low posterior mid-dorsal raised ridge. Urosome segment 1 with strong carination preceded by notch. Fused urosome segments 2 & 3 with low mid-dorsal carina. Head: rostrum medium, deflexed distally (<< 1/2 head length); anterior head lobe broad, upper angle acute. Eye medium (large in male). Antennae medium strong. Antenna 1, peduncular segment 2 shorter than 1, weakly setose (brush-setose posteriorly in male); segment 3 very short; accessory flagellum minute. Antenna 2 peduncular segments 4 & 5 margins moderately setose (segments 3 & 4 anteriorly brush setose in male).

Lower lip, inner lobes lacking. Mandible: molar strong; spine row with 6 blades and accessory setae; left lacinia 5-dentate; right lacinia bifid-flabellate; palp medium, segment

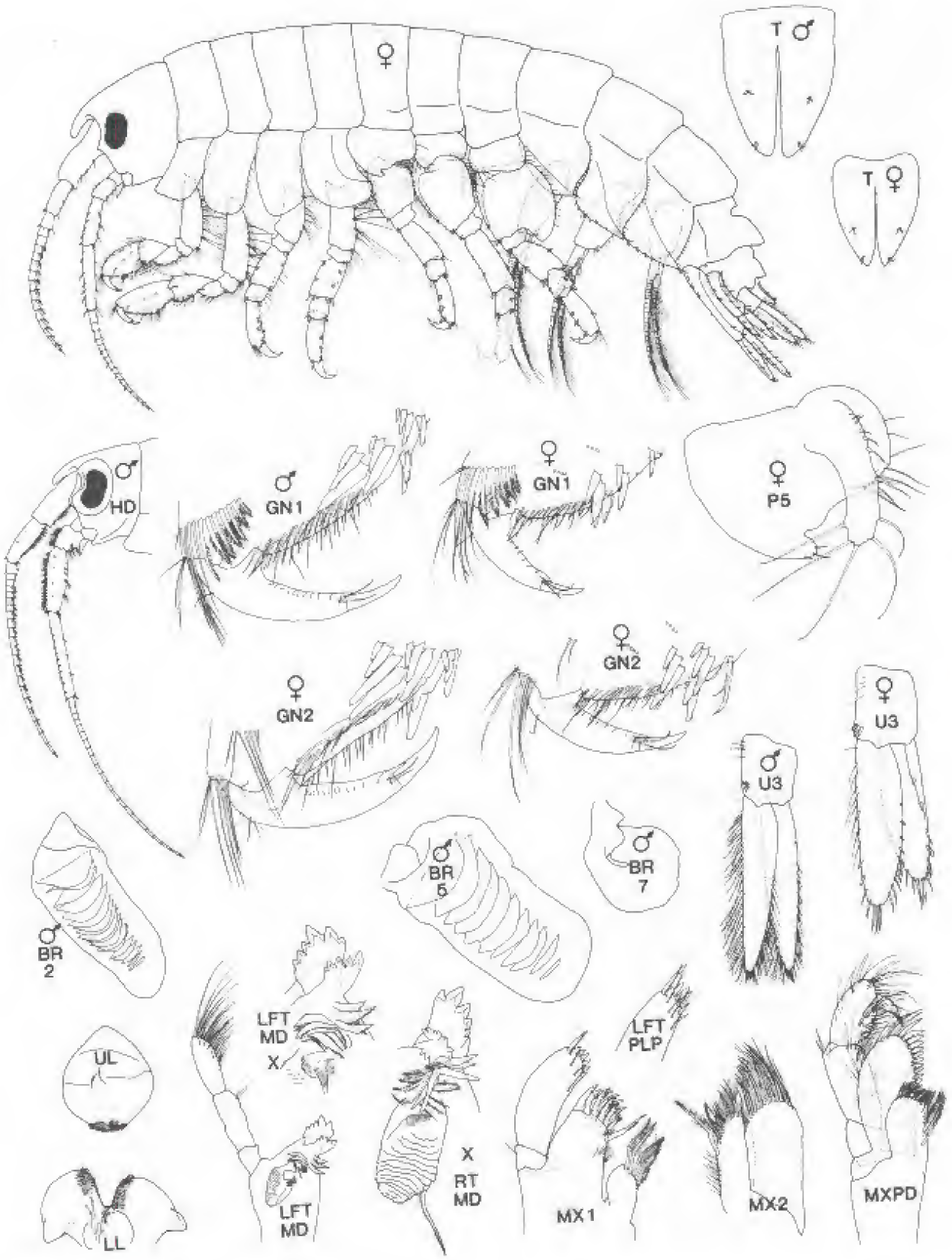

FIG. 10. ***Atylus borealis,*** **new species. Yakan Pt. Q. C. I., B. C. Male (20.0 mm) Fem. (13.0 mm)**

3 distally strongly setose. Maxilla 2, inner plate with 6 apical setae; palp medium, basal segment short. Maxilla 2, inner plate with single stout inner marginal plumose seta. Maxilliped ordinary, palp relatively short.

Coxae 1-4 medium large, lower margins convex; coxa 1 smallest, 4 largest. Coxa 5 deep, anterior lobe small, sharply rounded. Gnathopods 1 & 2 medium (more powerful than in *tridens*), slightly sexually dimorphic; bases strongly setose posteriorly. Gnathopod 1, carpus slightly shorter than propod; propod with antero-distal fan of 6-7 plumose setae and 3 clumps of stout spines at the postero-distal angle. Gnathopod 2 the larger; propod slightly longer than carpus, postero-distal angle with 3 clusters of spines in male, 2 clusters in female. Peraeopods 3 & 4 stout, spinose; segment 5 small, much shorter than segments 4 - 6; dactyls short. Peraeopods 5-7 short, stout, dissimilar; segment 5 small, much shorter than segments 4 and 6 (especially in peraeopod 6). Peraeopods 5 & 6 bases moderately broad, lower hind lobes very small. Peraeopod 7, basis broad, lower hind lobe deep, sharply rounded.

Pleopods powerful. Pleon plates 1-3, hind corners acuminate, slightly produced. Uropods 1 & 2 stout, rami unequal. Uropod 3, in female, rami broadly lanceolate, apices rounded, margins spinose and weakly setose; in male, rami narrowly lanceolate, apices subacute, margins richly setose.

Telson lobes medium, narrowing and not diverging distally, apices subacute, lacking spine(s).

Coxal gills large, on peraeopods 2-7, strongly pleated on 2-4 (male). Brood plates broadly strap-like.

Distributional Ecology: North-American endemic: southeastern Alaska to the Strait of Juan de Fuca. A species of summer-cold, high salinity, subtidal habitats.

Taxonomic commentary: The species has been described previously, as a large form of *A. tridens*, by Mills (1961), based on a female specimen taken at Telegraph Cove, Victoria, B. C. He summarized the differences between it and the true *Atylus tridens* in his Table 2. Although the two species are closely related, *A. borealis* differs not only in its larger size at maturity, but in its smaller eyes, more robust gnathopods and peraeopods, broader uropod rami, and shorter, unarmed telson lobes.

Variants: Specimens from whale pits in Pachena Bay cwere relatively small at maturity (6-9 mm) with short antennal flagellae, and sparesly setose and spinose.

Atylus collingi (Gurjanova)
(Fig. 11)

Nototropis collingi Gurjanova, 1938: 328, fig. 38.—Gurjanova, 1951: 638, fig. 476.
Atylus collingi Mills, 1961: 23, (part).—Austin, 1985: (part).—Barnard & Karaman, 1991: 263.

Material Examined (CMN collections, Ottawa):
ALASKA; Bering Sea region. St. Lawrence I., SE Cape, P. Slattery coll. July 10, 1980 - male (19.0 mm) (slide mt.), 1 male subadult, 1 female br II. (17.0 mm)(slide mts.); St. Paul I., June 25, 1983 - 18 specimens, incl. male (11.0 mm), female ov (9.0 mm).
S.E. ALASKA; ELB Stns, 1961 - ~190 specimens in 13 lots at: A8(1), A12(1), A30(32), A33(5), A43(~85), A48(1), AA63(1), A71(2) A80(6), A81(1), A84(1), A133(1), A140(~55).
BRITISH COLUMBIA:
Mainland Coast: ELB Stns, July, 1964: H13(11 - including male (11.0 mm) (slide mt.), female ov (8.5 mm) (slide mt.), H16(1), H17(21).

Diagnosis. Female br. III (17.0 mm), male (19.0 mm): Body large, strongly compressed. Peraeon and pleon with mid-dorsal ridge, elevated to low carina posteriorly on peraeon segments 6 & 7 and pleon segments 1-3. Urosome segment 1 with strong mid-dorsal crest. Fused urosome segments 1 & 2 with mid-dorsal crest, and weak dorsolateral ridges. Head: rostrum medium, nearly straight (~ 1/3 head length); anterior head lobe broad, slightly emarginate, upper angle subacute. Eyes small, lateral. Antennae relatively short, stout; flagella short. Antenna 1, peduncular segment 2 shorter than 1 (both sexes), posteriorly moderately setose (brush-setose in male); segment 3 medium; flagellum 12-segmented; accessory flagellum minute. Antenna 2, peduncular segments 4 & 5 stout, surfaced with numerous clusters of short setae; posterior margin with short setae (both sexes); peduncular segments 4 & 5 stouter and more elongate in male.

Lower lip, inner lobes very weak, not well defined. Mandible: molar strong; spine row with 5-6 narrow blades and accessory setae; left lacinia 5-dentate, right lacinia bifid, apices 3-5 dentate; palp strong, segment 3 distally setose. Maxilla 1, inner plate with 6-7 long apical setae; palp stout, proximal segment short. Maxilla 2, inner plate with 6-7 pectinate inner marginal setae. Maxilliped normal, inner plate relatively tall.

Coxae 1-4 large, deep, lower margins of 1-3 convex, of 4 subacute. Coxa 5 deep, anterior lobe small, rounded. Gnathopods 1 & 2 stout, subsimilar (2 larger), weakly sexually dimorphic, bases posteriorly strongly setose. Gnathopod 1, carpus short, hind lobe deep; propod with antero-distal group of 4-5 pectinate setae, and 6-7 rows of short stout spines (5 rows in female) at postero-distal angle; dactyls basally thick. Gnathopod 2, propod and carpus slightly larger and more elongate than in gnathopod 1.

Peraeopods 3 & 4 stout, spinose, 4 slightly heavier than 3; segment 5 small, shorter than segment 6 and much shorter than 4; dactyls medium(> 1/2 length segment 6). Peraeopods 5 - 7 dissimilar; segment 5 small, shorter than segment 6 and much shorter than segment 4. Peraeopods 5 & 6, bases moderately broadened, hind lobes moderate, not produced. Peraeopod 7, basis, postero-distal lobe rounded below.

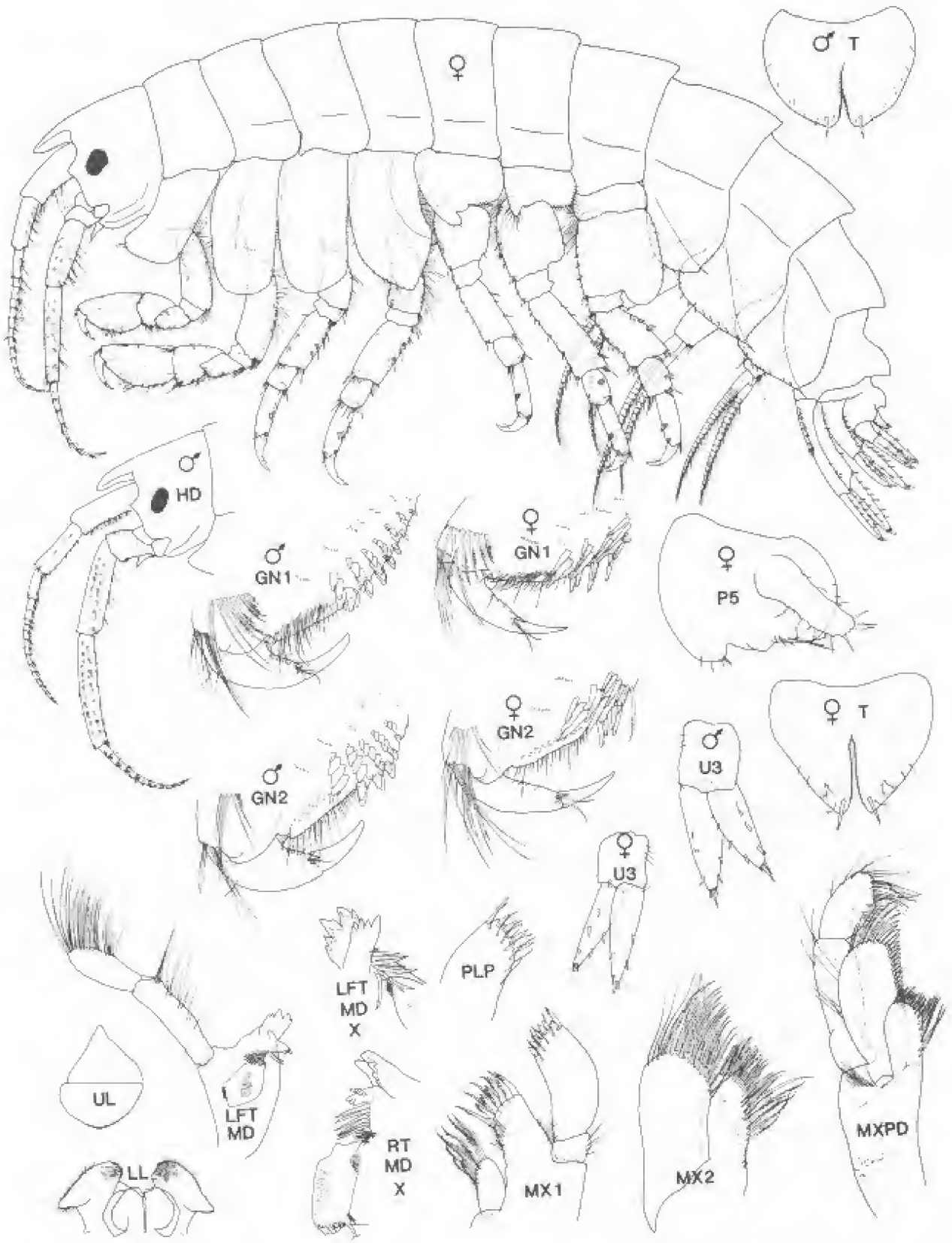

FIG. 11. ***Atylus collingi*** **(Gurjanova) St. Lawrence I. Bering Sea. Male (19.0 mm). Femalebr. III (17.0 mm).**

Pleopods stout. Pleon plates 1-3 broad, hind corners acuminate. Uropod 1 stout, rami subequal. Uropod 2, rami relatively long, unequal. Uropod 3, rami short (< 2X peduncle), apices acute, margins weakly spinose.

Telson lobes short (shorter in male), fused 1/3 basally, converging distally, apices each with single slender spine

Coxal gills on peraeopods 2-7, weakly pleated anteriorly, smaller, simple posteriorly, in males and females. Brood plates broadly strap-like.

Distribution: Japan Sea to the Chukchi Sea, in depths of 3-10 m. North American Pacific region: from the Bering Sea and Aleutian Islands south to the Strait of Juan de Fuca and Puget Sound.

Taxonomic Commentary: The western Pacific material figured by Gurjanova (1951) differs from North American material in its somewhat smaller, more acute coxal plates 1-4, deeper hind lobe of the basis of peraeopod 7, and inner plate of maxilla 2 that has only 3 apical setae.

Atylus georgianus, new species
(Fig. 12)

Atylus collingi Mills, 1961: 23, figs. 2, 4B A.—Staude, 1987: 382(part?).—Barnard & Karaman, 1991: 263 (part).

Material Examined (CMN collections, Ottawa):
BRITISH COLUMBIA: ELB material (1955, 1957, 1959) from the Queen Charlotte Islands and Vancouver I., reported upon by Mills (1961), has been re-examined, and proves to consist entirely of this species.

Additional material, from S. Vancouver I. inludes: ELB Stn. H43 (Witty's lagoon), July 28, 1964 - 17 imm. Saturna I., JFL Hart coll., Aug. 26, 1955 - female ov (8.0 mm). Holotype (slide mt.), CMN Cat. No. NMCC1994-0387; 1 male (7.5 mm), Allotype (slide mt.), CMN Cat. No. NMCC1994-0388; 10 other specimens, Paratypes CMN Cat. No. NMCC1994-0389. Head of Departure Bay, JFL Hart coll., Aug. 25, 1938 - 2 males (8.0 mm), 1 female br. III (9.0 mm).
WASHINGTON: North of Columbia estuary, ELB Stns, July, 1966 - 6 small specimens in 4 lots at: W26b(1), W35(2), W40(1), W46(2).

Diagnosis: Male (7.5 - 8.0 mm); female (8 - 9 mm): Body medium, laterally compressed. Peräeon and pleon with mid-dorsal ridge increasingly elevated to weak posterior carina on peraeon segments 6-7, and pleon segments 1-3. Urosome segment 1, and fused segments 2 & 3, each with single elevated rounded tooth. Head: rostrum short, extending little beyond weakly acute anterior head lobe. Antennae medium, much as in *A. collingi*, but shorter and less setose.

Lower lip, inner lobes small. Mandible: molar medium; spine row with 6-7 slender blades and accessory setae; left lacinia strongly 5-dentate; right lacinia simply bifid; palp slender, segment 3 setose apically. Maxilla 1, inner plate with 5 apical setae; palp medium slender. Maxilla 2, inner plate with single inner marginal plumose seta. Maxilliped slender, basal segment with long distal facial setae.

Coxae 1-4 large, deep, overlapping, rounded below. Coxa 5 deep, anterior lobe small rounded. Gnathopods 1 & 2 medium (less strong than in *A. collingi*); slightly sexually dimorphic; bases setose posteriorly. Gnathopod 1, carpus very short, lobe deep; propod with antero-distal group of 3-5 pectinate setae, and 4 groups of slender spines at postero-distal angle. Gnathopod 2, propod and dactyl larger, heavier than in gnathopod 1.

Peraeopods 3 & 4 medium strong, margins spinose; segment 5 small, much shorter than segments 4 & 6, dactyls medium. Peraeopods 5-7 medium, less spinose, dissimilar; segment 5 much shorter than segments 4 & 6. Peraeopods 5 & 6, hind lobes of basis small or lacking. Peraeopod 7, basis, hind lobe rounded below.

Pleopods medium. Pleon plates 1-3, hind corners squarish, not acuminate. Uropod 1, rami subequal. Uropod 2, rami unequal. Uropod 3 short, rami ~2X length of peduncle, margins spinose (both sexes).

Telson lobes short, fused in basal 1/3, converging distally, apex of each with slender spine. Coxal gills sac-like, anterior gills pleated in male, simple in female.

Etymology: The trivial name *georgianus* alludes to the Strait of Georgia where the species is commonly encountered.

Distribution: Endemic to the North American Pacific coast: Queen Charlotte Islands and central B. C., Strait of Georgia, to Washington-Oregon coast, frequently in beds of eel grass, in sandy shallows.

Taxonomic Commentary: *Atylus georgianus* is closely related to *A. collingi* Gurjanova but differs in mandibular palp, armature of plates of the maxillae, size of gnathopods, and shape of the uropomal carinae. The subequal size of the mature male and female is distinctive.

Atylus occidentalis Hirayama

Atylus occidentalis Hirayama, 1986: 4, figs. 1-4.— Ishimaru, 1994: 42.

Taxonomic Commentary. The original material was from Otsuchi Bay, Japan. We tentatively accept the designation of this species by Hirayama and Ishimaru (loc. cit), as a member of the genus Atylus (sens. str.). Regretably, however, we have seen no material of this species, and the literature is not available to us. The species is therefore not included to the regional key (p. 10) or analysis of species relationships (p. 58-59).

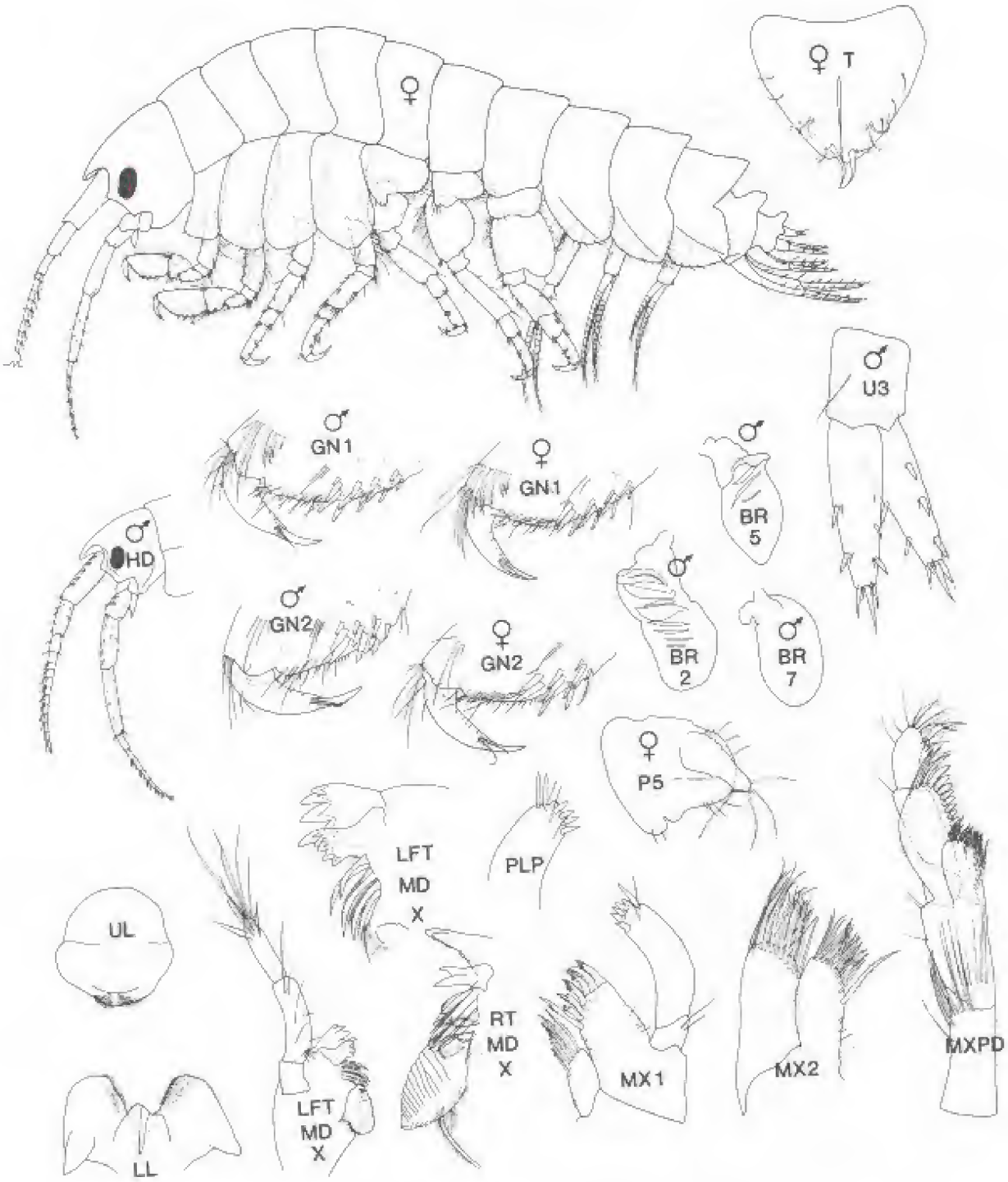

FIG. 12. ***Atylus georgianus,*** **new species. Saturna I., B. C. Fem. ov. (8.0 mm) Male (7.5 mm)**

KEY TO GENERA OF NOTOTROPIINAE

1. Pigmented eyes well developed; anterior head lobe blunt or slightly emarginate; peraeopods 3 & 4, segment 4 small, much shorter than segments 4 & 6; coxal plates 1-4 large, deep, strongly overlapping . . . . . ***Nototropis*** (p. 28)

—Pigmented eyes lacking; anterior head lobe bifid; peraeopods 3 & 4, segment 4 slightly shorter than segments 4 & 6.; coxal plates 1-4 small, shallow, basally overlapping only . . . . . ***Aberratylus*** (p. 30)

Nototropiinae, new subfamily
(see Fig. 1(b))

Atylidae (part) Stebbing, 1906: 329.—Barnard, 1969a: 161.—Gurjanova, 1951: 327.
Atylidae Lincoln, 1979: 438.
Dexaminidae (Dexamininae) (part) Bellan-Santini, 1982: 212.—Barnard & Karaman, 1991: 260.

Type genus: *Nototropis* Costa, 1853: 170.

Genera: *Aberratylus*, new genus (p. 30).

Diagnosis: Similar to Atylinae (p. 8) with the following differences: Body medium, occasionally large. Peraeon, posterior segments often not mid-dorsally toothed or carinate. Pleon various, often smooth above. Urosome 1 usually with mid-dorsal tooth and preceding sharp notch. Rostrum short to medium. Eyes large (when present). Antennae slender; antenna 1, peduncular segment 2 longer than 1.

Mouthparts basic. Lower lip, inner lobes variously developed, or lacking. Mandible, molar strong, palp slender, 2-3 segmented, weakly setose.

Coxal plates 1-4 large, lower margins smooth or rounded. Gnathopods 1 & 2 subsimilar, moderately to strongly subchelate (esp. in male), variously sexually dimorphic, or not.

Peraeopods 3 & 4 distinctly unequal in size, peraeopod 4 the smaller, shorter in segments 2, 5 & 6; segment 5 variable, but typically small, much shorter than segments 4 & 6; segments 2, 4, and 6 (male) often posteriorly armed with "swimming setae". Peraeopod 5, basis, posterior lobe usually produced below. Peraeopods 5-7, segment 5 not shortened, 5 & 6 subequal; segment 4 often elongate.

Pleopods powerfully developed, stronger in the male. Pleon plates 1-3, hind corners mucronate. Uropod 3, rami long, lanceolate, margins variously setose (both sexes).

Telson, lobes ordinary, deeply separated, apices spinose.

Coxal gills 2-5 strongly phylloform or dendritic (especially in male), simple on peraeopods 6 & 7. Brood plates medium to strap-like.

Taxonomix Commentary: The subfamily overlaps with subfamily Atylinae in a number of character states, but can be distinguished reliably by the combination of character states illustrated in Fig. 1(b) (p. 6).

Nototropis Costa
(see Fig. 13)

Nototropis Costa, 1853: 170.—Stebbing, 1906: 329.—Gurjanova, 1951: 680 (most).
Atylus Lincoln, 1979: 438 (part).—Barnard, 1969: 163 (part).—Bellan-Santini, 1982: 212 (all).—Barnard & Karaman, 1991: 262 (part).
Paratylus G. O. Sars, 1895: 462.

Type species: *Nototropis guttatus* Costa 1953 (=*Nototropis spinulicauda* Costa).

Species: *Nototropis brevitarsus* Ledoyer; 1979; *N. comes* Giles, 1888; *N. dentatus* Schellenberg, 1931; *N. falcatus* (Metzger, 1871); *N. granulosus* Walker, 1904; *N. homochir* (Haswell, 1885); *N. massilensis* Bellan-Santini, 1975; *N. megalops* (Moore, 1984); *N. melanops* Oldevig, 1959; *N. minikoi* Walker, 1905; *N. nordlandicus* Boeck, 1871; *N. reductus* K. H. Barnard, 1930; *N. serratus* Schellenberg, 1925; *N. smitti* Goes, 1866; *N. swammerdamei* Milne-Edwards, 1830; *N. taupo* J. L. Barnard, 1972; *N. urocarinatus* McKinney, 1980; *N. vedlomensis* Bate & Westwood, 1863; *Nototropis* sp. (=*N. guttatus* Irie, 1965)?

Diagnosis: Small to medium (occasionally large) atylids. Rostrum short to medium. Eyes often very large, especially in males. Peraeonal segments 5-7 and pleon segments 1-3 dors-ally smooth, occasionally mucronate Urosome 1 dorsally with carina and preceding notch; fused urosome segments 2 & 3, median dorsal carina variously developed or lacking. Antenna 1, peduncular segment 2 not shorter than segment 1; accessory flagellum minute or scale-like. Antenna 2, peduncular segments 4 & 5 strong, weakly marginally setose.

Lower lip, inner lobes various, occasionally lacking. Mandible, palp slender, (2)3-segmented. Maxilla 1, inner plate with 3-8 apical setae; palp (1)2-segmented; Maxilla 2, inner plate with stout inner marginal plumose seta. Maxilliped, palp normal, slender.

Coxal plates 1-4 regular, medium, lower margins rounded or straight, not acute. Coxa 5 anterolobate, lobes rounded below. Gnathopods 1 & 2 variously sexually dimorphic; carpus and propod relatively short, subequal in length; propod of gnathopod 1 with antero-distal clusters of pectinate setae.

Peraeopod 4 distinctly smaller or shorter than peraeopod

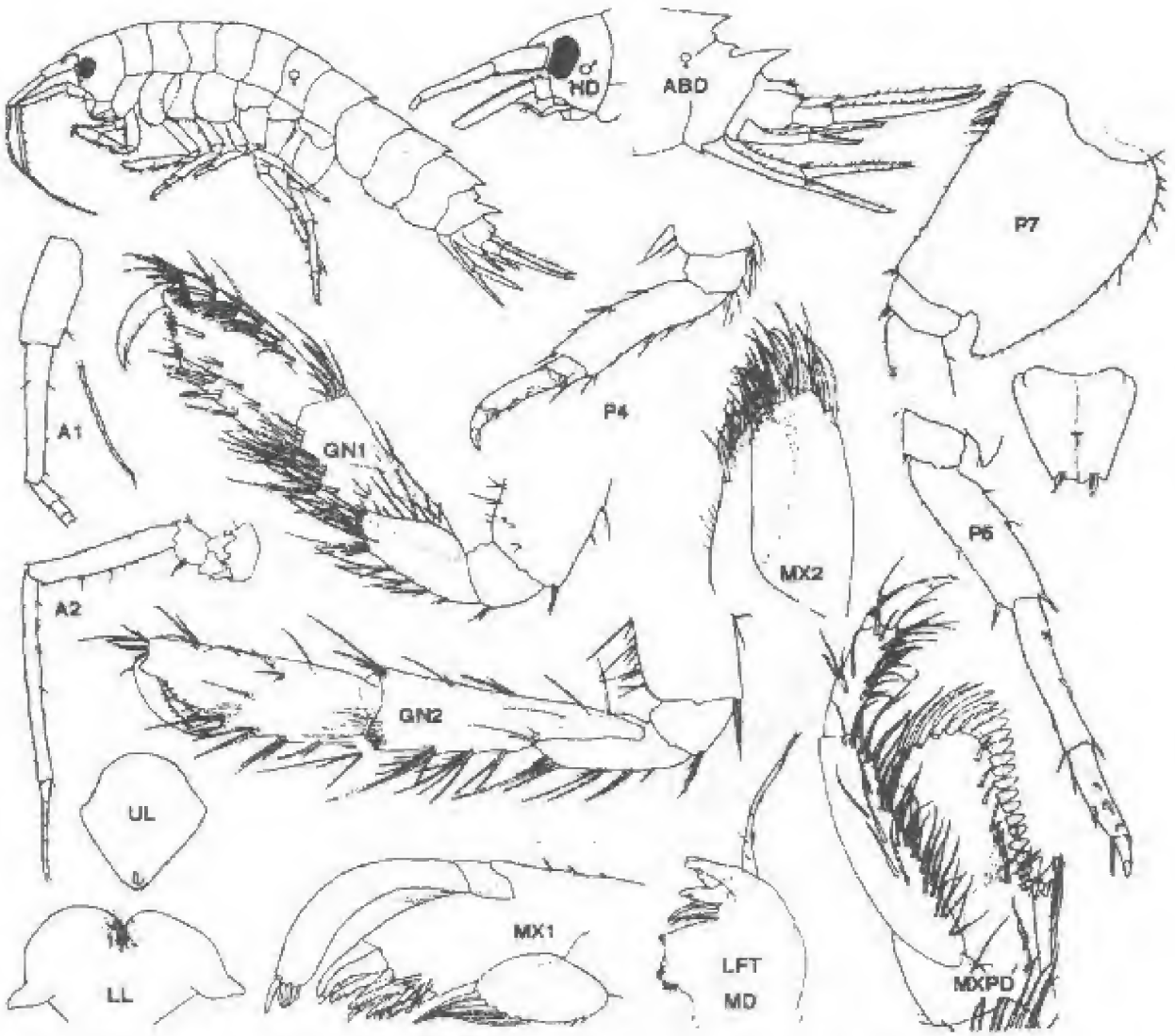

FIG. 13. ***Nototropis guttatus*** **Costa, 1853. Female (9-11 mm) Mediterranean Sea. (modified from Bellan-Santini, 1982)**

3; segment 5 (in both) usually much shorter than segments 4 & 6; in male, anterior and posterior margins of segments 4-6 and distal portion of segment 2 often lined with "swimming" setae.. Peraeopods 5-7 not strongly dissimilar in size and form; bases, hind lobes strong, often acute below; segment 5 large, usually longer than segments 4 and/or 6; dactyls medium.

Pleopods strong. Pleon side plates, hind corners acuminate, not produced. Uropod 1 rami subequal in length. Uropod 2, outer ramus the shorter. Uropod 3, rami strong, lanceolate, subequal, margins setose in male, spinulose and or setose in female. Telson regular, lobes medium, apices obliquely truncate.

Brood plates medium to broad, margins simple-setose. Anterior (peraeopods 2-5) coxal gills strongly dendritic or phylliform, especially in the male.

Variables: Rostrum large (*N. smitti*); anterior peraeonal segments dorsally carinate (*N. homochir*); gnathopod 2, propod and dactyl elongate (*N. taupo, N. smitti*); peraeopod 7, basis, postero-distal lobe weak or lacking (*N. homochir, N. melanops, N. smithi*; urosome weakly or not carinate (*N. megalops*); telson lobes short (*N. smitti*). Further generic and/or subgeneric categories may yet be required to reflect the taxonomic significance of these variables.

Distributional Commentary: Component species of *Nototropis* are strongly tethyan in distribution, occurring mainly in tropical and warm temperate coastal waters of the Mediterranean-Caribbean Atlantic and Indian oceans, with a few morphologically aberrant outliers in arctic and austral regions. To date, one species, implausibly identified as the Mediterranean species *N. guttatus* Costa by Irie (1965) represents a questionable record of this genus and subfamily from Japanese waters. None was identified in present study material from the North American Pacific region.

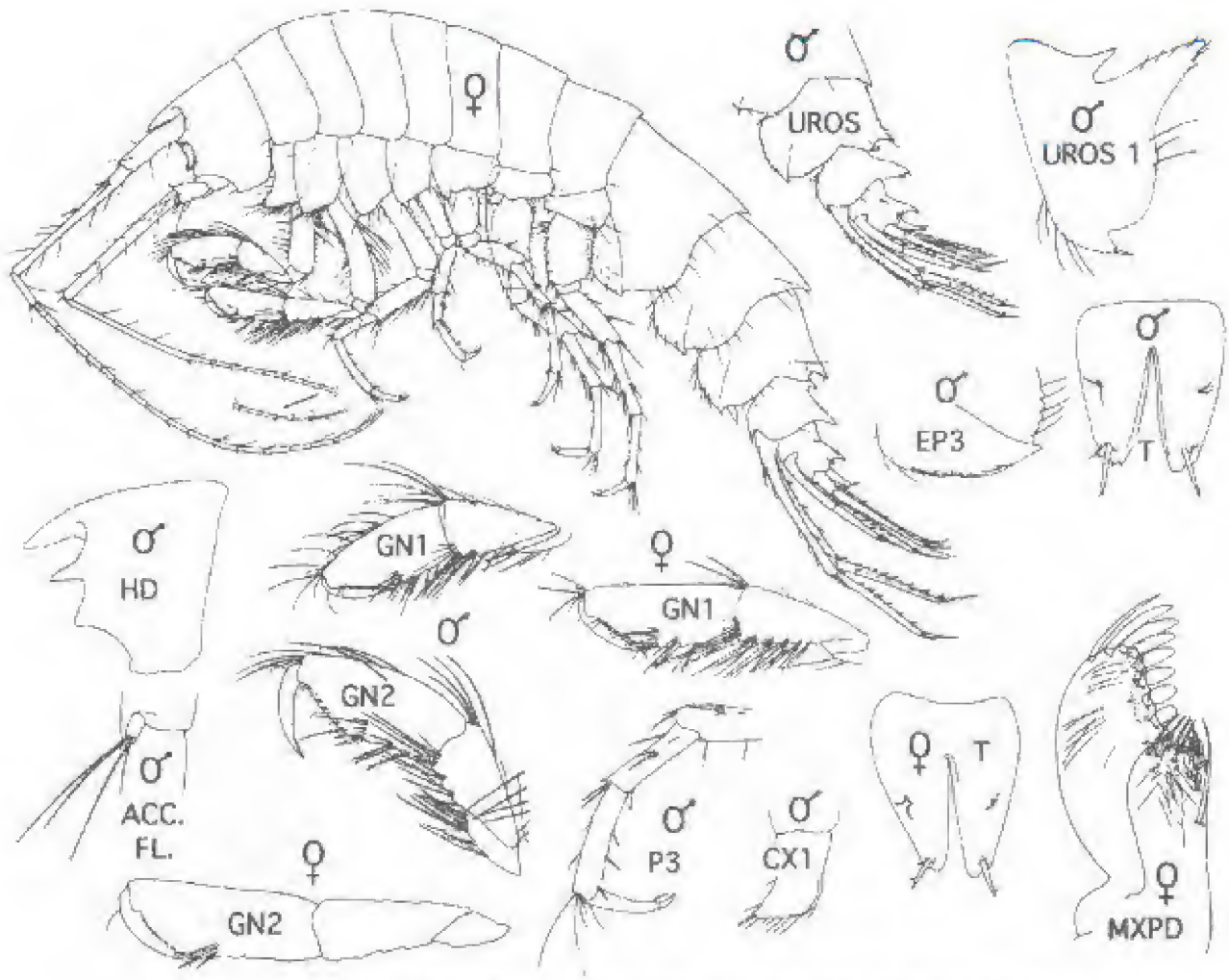

FIG. 14. *Aberratylus aberrantis* (J. L. Barnard). Female (4.8 mm) Male 6.1 mm) (Modified from Barnard, 1973)

Aberratylus , new genus
(see Fig. 14)

Arylus J. L. Barnard, 1962: 69 (part.);
Lepechinella J. L. Barnard, 1973: 7 (part).—Barnard & Karaman, 1991: 261(part).

Type species: *Arylus aberrantis* J. L. Barnard, 1962: 69, figs. 66, 67.—Barnard, 1964: 40, fig. 32. (=*Lepechinella aberrantis* J. L. Barnard, 1973: 7, figs.).

Diagnosis: Rostrum medium. Peraeon segments 1-6 smooth dorsally. Peraeon segment 7 and pleon segments 1-3 posterodorsally mucronate. Urosome segment 1 middorsally with two teeth and intermediate notch; fused urosome segment 2 & 3 with prominent carina. Anterior head lobe weakly bifid. Pigmented eyes lacking. Antenna 1, peduncular segment 2 slender, elongate; accessary flagellum 1-segmented. Antenna 2 peduncular segments slender, elongate, weakly setose.

Lower lip, inner lobespresent Mandible, palp weak, segment 3 short; axilla1, palp broad, 2-segmented; inner plate with 2 apical setae. Maxilla 2, inner plate with single inner marginal plumose seta. Maxilliped, palp and plates normal.

Coxal plates 1-4 small, basally contiguous or overlapping, lower margins entire, denticulate, not acute or processiferous. Coxa 5 anterolobate, anterior lobe various . Gnathopods 1 & 2 subsimilar (2 larger), very weakly sexually dimorphic; carpus and propod medium, palms very oblique.

Peraeopods 3 & 4 slender, but relatively short; segment 5 slightly shorter than segments 4 & 6; dactyls medium. Peraeopods 5-7 dissimilar in size; bases little broadened, lower hind lobes small, not acute; segments 4 & 5 subequal in length, both shorter than 6; dactyls medium (= segment 6)

Pleon plates 1-3 broad, hind corners mucronate. Uropods slender; uropod 1, rami subequal; uropod 2, outer ramus the shorter. Uropod 3, rami slender lanceolate, inner margins weakly setose.

Telson ordinary, lobes medium length, not diverging, apices with single spine.

Coxal gills not described (probably pleated). Brood plates not described.

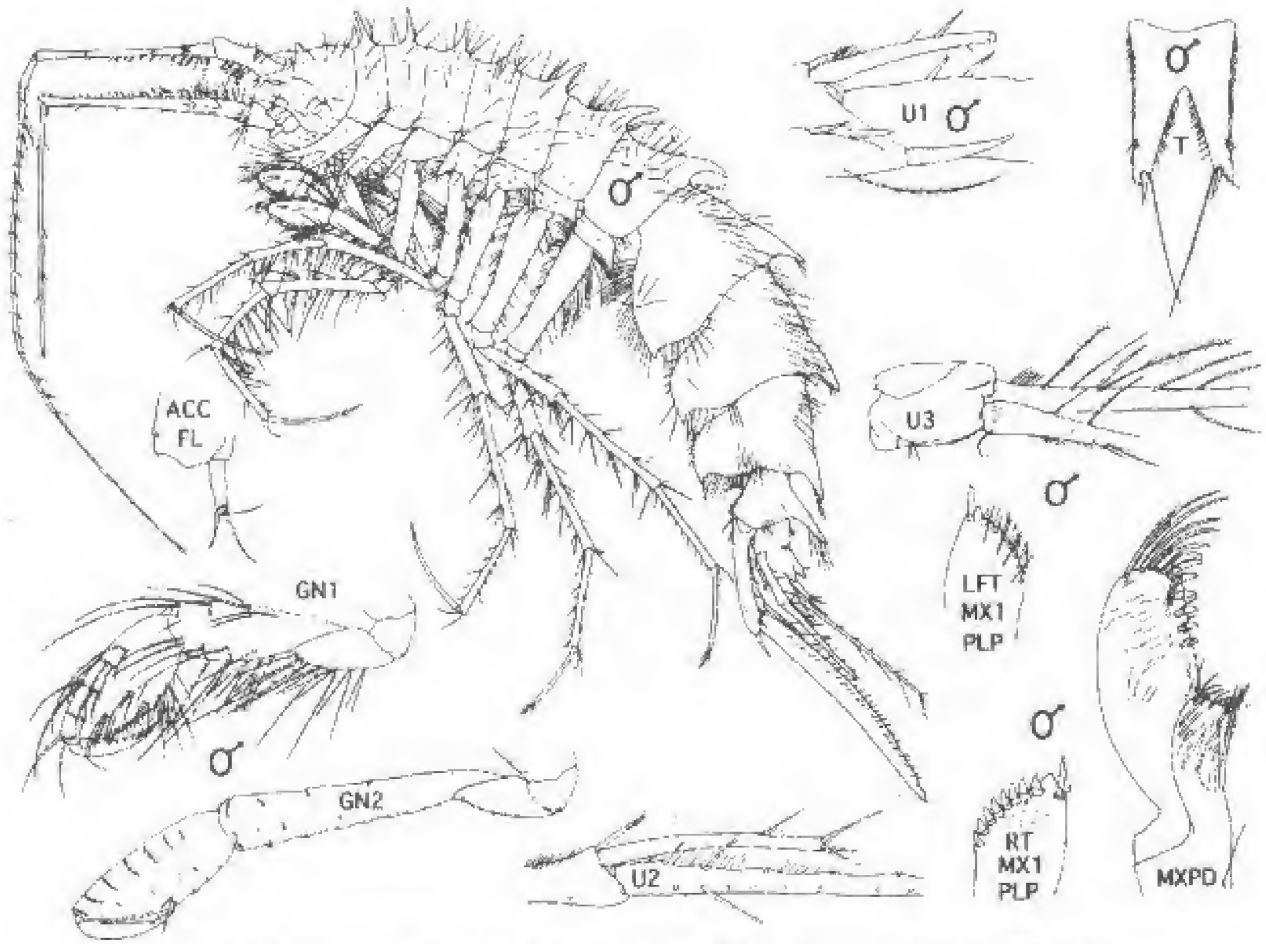

FIG. 15. *Lepechinella uchu* J. L. Barnard Male (7.6 mm) Female (8.5 mm) (modified from Barnard, 1973)

Lepechinellinae Schellenberg (revised status)
(see Figs. 1(c); 15)

Lepechinellidae: Schellenberg, 1926: 344.—Gurjanova, 1951: 674.—Barnard, 1969: 286.—Bousfield, 1982: 278. Dexaminidae (part): Barnard, 1973a: 5.—Bellan-Santini, 1982: 212.—Barnard & Karaman, 1991: 260.

Diagnosis: Peraeon (variously) and pleon segments mid-dorsally processiferous and/or densely covered with small setae and spines. Urosome 1 with single mid-dorsal process. Urosome 2 & 3 not carinate. Head, rostrum spike-like; antero-lateral head margin acutely bifid. Pigmented eyes lacking. Antennae long, slender (both sexes); antenna 1 the shorter; peduncular segment 2 long; accessory flagellum present, 1-segmented.

Lower lip, inner lobes well developed. Mandible, palp slender, reduced. Maxilla 1, palp 2-segmented, distal segment broadened. Maxilla 2, inner plate narrow. Maxilliped, outer plate large; inner plate arched disto-medially; palp 4-segmented.

Coxa plates 1-7 narrow, small, separated basally. Coxae 1-4 incised or acute, often bilobate below; coxa 1 distinctly deepest; coxa 5 small, anterolobate. Gnathopods slender, weakly or not subchelate; carpus (especially in gnathopod 2) longer than propod.

Peraeopods 3-7 slender, elongate. Peraeopods 4 slightly shorter than 3, mainly in basis; segment 5 little (or not) shortened; dactyls elongate (often >segment 6). Peraeopods 5-7 subsimilar in form and size; bases sublinear.

Pleopods slender, elongate. Uropods 1 & 2 slender. Uropod 1, outer ramus enlarged. Uropod 2; outer ramus not shortened. Uropod 3, rami sublinear, rod-like, margins sparsely (or not) setose, apices spinose.

Telson lobes short to medium, fused basally by more than 1/3; apices usually diverging, distally narrowing. Coxal gills pleated.

Genera: *Lepechinella (Lepechinella)* Stebbing, 1908: 191; *Paralepechinella* Pirlot, 1933: 161; *Lepechinelloides* Thurston, 1980: 81; *Lepechinellopsis* Ledoyer, 1982: 365.

Taxonomic and Biogeographic Commentary: *"Lepechinella" aberrantis* J. L. Barnard, 1964, is basically an atylid that exhibits a very few "lepechinellid" character states (of head, peraeopods 3 & 4, and uropod 3). Accordingly, the species is here reassigned within family Atylidae

KEY TO GENERA AND SUBGENERA OF LEPECHINELLINAE

1. Mandibular palp segment 3 elongate, telson lobes not diverging. . . . . ***Paralepechinella***
—Mandibular palp segment 3 short or lacking, telson lobes diverging . . . . . 2.

2. Cephalic projections lacking; mandibular palp 1-segmented . . . . . ***Lepechinelloides***
—Cephalic projections prominent; mandibular palp 3-segmented . . . . . 3.

3. Outer ramus of uropods 1-3 reduced . . . . . ***Lepechinellopsis***
—Outer ramus of uropods 1-3 normal . . . . . ***Lepechinella***

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to subfamily Nototropiinae with which it appears to have closest morphological affinities (p. 28). A new genus, *Aberratylus* (p. 30) is here erected to accommodate its unique combination of character states.

The phyletic and artificial keys to *Lepechinella* developed by Barnard (1973) suggest further internal subgroupings that might merit formal subgeneric recognition. Thus, a group containing *Lepechinella auca*, *L. cachi*, *L. cetrata*, and *L. huaco* exhibits plesiomorphic (atylinid) character states including a lack of mid-dorsal teeth on three or more peraeonal segments, coxae 1-4 weakly processiferous below, and peraeopod dactyls less markedly elongate than in other lepechinellid species groups.

About 35 described species, in 4 genera, can be assigned to subfamily Lepechinellinae, all abyssal and bathypelagic-epibenthic. At least two species are known from abyssal depths off Japan (Gamo, 1981). None was recorded from the Cascadia Abyssal Plain off the coast of Oregon by Dickinson and Carey (1978), at least not in significant numbers, and none was found in CMN amphipod material from other North American Pacific deep-water sites.

Subfamily Anatylinae Bulycheva (Revised status)
(Figs. 1(d); 16)

Anatylidae Bulycheva, 1955: 205.
Dexaminidae (Anatylinae) Barnard, 1969a: 202.
Dexaminidae (part) Barnard & Karaman, 1991: 260.

Type Genus: *Anatylus* Bulycheva 1955: monotypy.

Genera: *Kamehatylus* Barnard, 1970b: 93 (revised status).

Diagnosis: Small atylids (3-6 mm). Body thin. Peraeon segments 5-7 and pleon segments 1-3 variously carinate or smooth mid-dorsally. Rostrum weak. Anterior head lobe shallowly excavate. Pigmented eye small. Antennae 1 & 2 short; flagella short, 4-5 segmented. Antenna 1, peduncular segments 1 & 2 subequal; accessory flagellum vestigial. Antenna 2, peduncular segments weakly setose.

Lower lip, inner lobes very weak. Mandible: molar trending to reduction; left lacinia 4-dentate; palp lacking. Maxilla 1, inner plate with 2 apical setae; palp slender. Maxilla 2, inner plate slender. Maxilliped normal; palp strong, 4-segmented.

Coxae 2-4 relatively shallow, narrow, lower margins gently excavate. Coxa 1 tapering, subacute below. Coxa 5 shallow. Gnathopods 1 & 2 slender, dissimilar in size; propod, palms very oblique. Gnathopod 1, propod and carpus relatively short. Gnathopod 2, carpus elongate.

Peraeopods 4 distinctly shorter than 3, mainly in basis and segments 5 & 6; segment 5 short. Peraeopods 5-7 bases dissimilar, lower lobes very small or lacking; segment 5 not shortened, longer than segment 6.

Pleon plate 1-3 deep, hind corners obtuse or rounded. Uropods 1 & 2, rami medium, unequal. Uropod 3 short, rami stout, margins spinose.

Telson medium short, lobes deeply separated, converging distally, apices with single spine.

Coxal gills undescribed, but probably sac-like, unmodified. Brood plates undescribed, probably strap-like. Male undescribed.

Taxonomic and Distributional Commentary: To date, the subfamily contains but 5 described species in two closely similar genera, of Indo-Pacific and western Pacific affinities, as detailed below. The present study restores the group to the subfamily status proposed initially by Barnard (1969a).

Anatylus Bulycheva

Anatylus Bulycheva, 1955: 205, original designation.—Barnard, 1969a: 202 (in Dexaminidae)
Atylus (part) Barnard & Karaman, 1991: 262.

Type Species: *Anatylus pavlovski* Bulycheva, 1955.

Diagnosis: Body medium, thin. Peraeon, segments 5-7 and pleon segments 1-3 carinate along dorsal margin (cf. *Atylus levidensus*). Rostrum medium strong. Anterior head lobe shallowly excavate. Pigmented eye small, round. Antennae 1 & 2 short flagella 4-5 segmented. Antenna 1, peduncular segments 1 & 2 subequal; accessory flagellum vestigial. Antenna 2, peduncular segment 5 longest.

Lower lip, inner lobes present, moderate. Mandible: palp lacking; molar reduced, weakly triturative. Maxilla 1, inner plate fused to base of outer plate, with 2 apical setae; palp 2-segmented. Maxilla 2, inner plate small, lacking strong plumose inner marginal seta. Maxilliped normal, palp

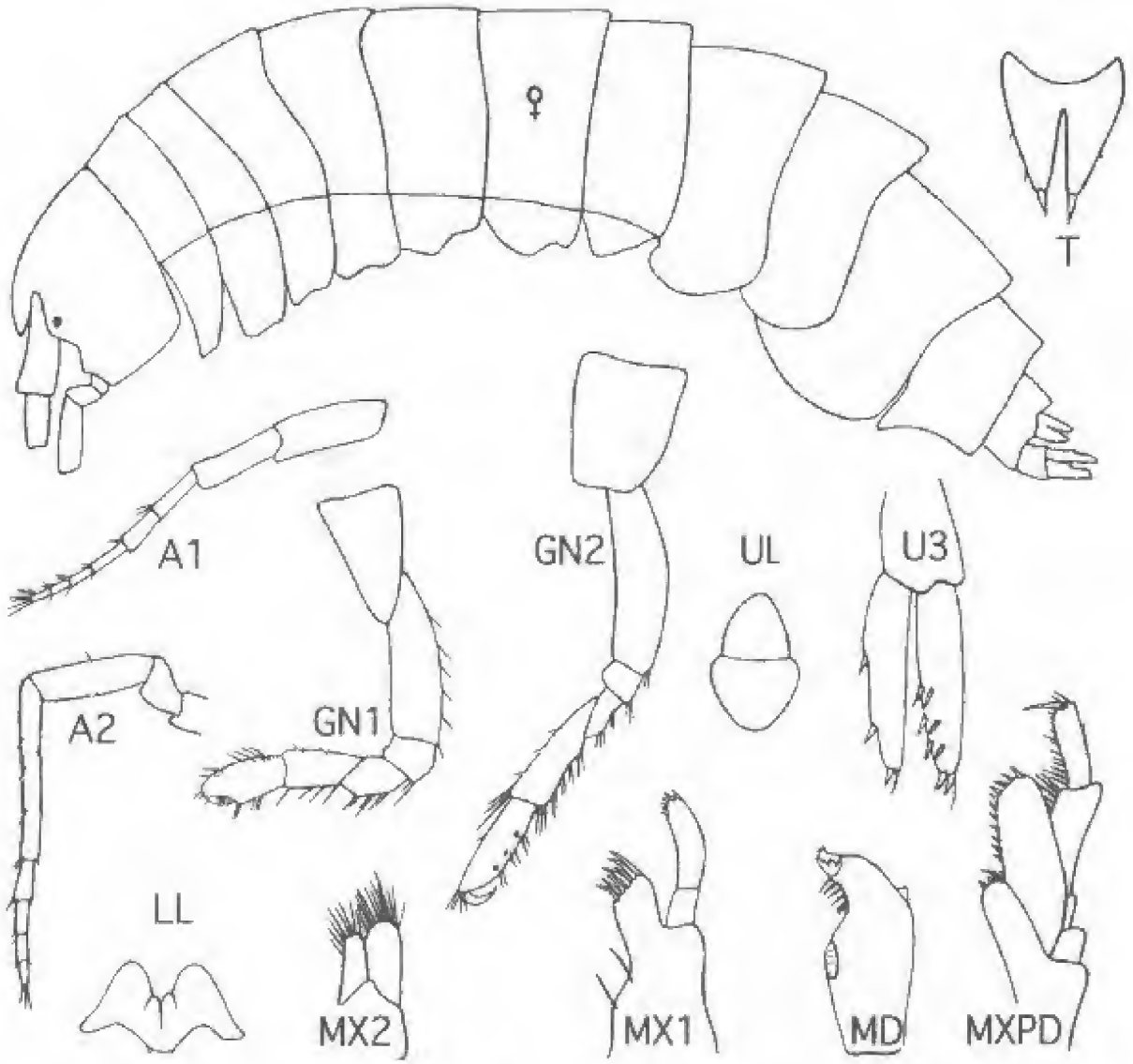

FIG. 16. *Anatylus pavlovskii* Bulycheva, 1955. Female (6-8 mm) Japan Sea (modified from Bulycheva, 1955)

strong, 4-segmented.

Coxae 2-4 relatively shallow, narrow, slightly emarginate below. Coxa 1 tapering, subacute below, almost as deep as coxa 2. Coxa 5 broadly antero-lobate. Gnathopods 1 & 2 slender, dissimilar in size (2 larger); carpus longer than propod, palms very oblique. Gnathopod 1, propod and dactyl relatively short. Gnathopd 2, propod and dactyl relatively long, slender.

Peraeopods 3 & 4, segment 5 shortened. Peraeopods 5-7 slightly dissimilar, segment 5 not described. Peraeopod 7, basis lacking distinct postero-distal process.

Pleopods not described, (not powerful?). Pleon plate 3 deep, rounded below. Uropods 1 & 2 not described.

Uropod 3 short, rami heavy, lanceolate, margins sparsely spinose(female). Telson medium short, lobes deeply separated, converging distally, apices each with single spine.

Coxal gills and brood plates undescribed.

Anatylus pavlovskii Bulycheva
(Fig. 16)

Anatylus pavlovskii Bulycheva, 1955: 206, fig. 6.—Bulycheva, 1957: 104.—Tzvetkova, 1967: 173.
Atylus pavlovskii Barnard & Karaman, 1991: 262, fig. 50A.

Diagnosis: With the characters of the genus

Distribution: The monotypic species *A. pavlovskii* is known only from the Russian portion of the Japan Sea (Peter-the-Great Bay), in medium depths (Bulycheva, 1955).

Taxonomic Commentary: As figured and described by Bulycheva (1955) and refigured by Barnard & Karaman (1991), this species bears a combination of character states

that are remarkably similar to those of *Kamehatylus*, originally diagnosed as a subgenus of *Atylus*, based on the Hawaiian species *K. nani* (below). Regretably, Bulycheva did not fully describe or figure the diagnostic character states of peraeopods 3-7. Until further material can be studied, the diagnostic subfamily character states are assumed to be similar to those of *Kematylus japonicus* which occurs at other localities in the Sea of Japan. The two genera appear closely similar in described character states, although the type of *Kamehatylus* is based on a species with all three urosomites fused. Whatever future studies reveal in this regard, the name *Anatylus* Bulycheva 1955 would be a senior synonym and is therefore retained here as a valid full genus.

Kamehatylus J. L. Barnard, revised status
(see Figs. 1(d); 17A,B)

Atylus (Kamehatylus) J. L. Barnard, 1970b: 93.—Ledoyer, 1979b: 157.—Barnard & Karaman, 1991: 262.

Type species: *Atylus (Kamehatylus) nani* J. L. Barnard, 1970b: 93, figs. 48, 49.

Species: *Kamehatylus japonicus* (Nagata, 1961); *K. processicer* (Siviprakasam, 1970); *K. tulearensis* (Ledoyer, 1984)?

Diagnosis: Small, morphologically modified atylids. Rostrum short. Eyes small. Peraeon and pleon dorsally weakly carinate or nearly smooth. Urosome segments 1, and fused 2-3 dorsally toothed; all three urosome segments fused in the type species. Antennae short, slender, flagella few-segmented; accessory flagellum lacking. Antenna 1, peduncle 1 with posterodistal tooth or process. Antenna 2, peduncular segments 4 & 5, margins nearly smooth.

Lower lip lacking inner lobes. Mandible: palp absent; molar process medium; spine row with 2-3 blades and accessory setae; left lacinia 4-dentate, right lacinia bifid-flabellate. Maxilla 1, inner plate with 2-3 apical setae; outer plate with 10 apical spines; palp slender, 2-segmented. Maxilla 2, inner plate, inner margin subapically with single large plumose seta. Maxilliped, palp slender, shortened.

Coxae 1-4 short, shallow, lower margins rounded or slightly incised. Coxa 1 subacute below. Coxa 5, anterior lobe small. Gnathopods 1 & 2 slender, dissimilar, probably little or not sexually dimorphic. Gnathopod 1, propod shorter than carpus, with antero-distal median facial clusters of pectinate setae. Gnathopod 2, carpus slender, longer than in gnathopod 1.

Peraeopod 4 distinctly smaller in size than peraeopod 3; segment 5 (of both) small, much shorter than segments 4 & 6; dactyls short. Peraeopods 5-7 subsimilar in size, bases not broadly expanded, lower hind lobes small or lacking; segment 5 not shortened, longer than segment 6, but not markedly longer than segment 4; dactyls short.

Pleon plates 1-3 regular hind corners mucronate. Pleopods not described. Uropods 1 & 2 slender, rami unequal. Uropod 3 rami short, subequal, margins spinose.

Telson lobes deeply separated, diverging distally, apices singly spinose, outer margins bare. Coxal gills sac-like, simple. Brood plates strap-like, not broad.

Mature male (Ledoyer, 1979b): Eye slightly larger, antennal flagella longer, than in female.

Taxonomical and Distributional Commentary. The few described species of this genus are essentially Indo-Pacific in distribution, northwards in the Pacific to southern Japan, but not yet recorded from the North American Pacific coast. The species appear morphologically specialized for a cryptic life style on coral reefs, in association with large, sessile invertebrates such as sea lilies (Siviprakasam, 1970).

Kamehatylus japonicus (Nagata)
(Fig. 17A)

Atylus japonicus Nagata, 1961: 216, figs. 1, 2.—Nagata, 1965a: 202, fig. 19.—Barnard & Karaman, 1991: 263.
non *Atylus (Kamehatylus) japonicus*—Ledoyer, 1979b: 156 fig. 7(II).

Taxonomic Commentary: The species has been well described and figured by Nagata 1961-1965, loc. cit) whose figures are partly reproduced here (Fig. 17A). Nagata's species conforms closely with the subgeneric diagnosis of Barnard (1970b) that was based on the Hawaiian species, *K. nani*. However, in the Japanese species, the posterior peraeon and pleon are more strongly carinated, urosome segment 1 is not fused with segments 2 & 3, and the gnathopods are more slender. Despite these and other minor differences, the authors consider Nagata's material from Japan congeneric with that of Barnard, and have broadened the generic diagnosis to accommodate both species.

Ledoyer (1979b, loc cit) described a very similar species from the Moluccas Islands, Indian Ocean, to which he had perceptively assigned the name *Atylus (Kamehatylus) japonicus* Nagata. Ledoyer's figures, reproduced here (Fig. 17B), do show remarkable similarities to those of Nagata, including the relatively small eye and excavate anterior head lobe, the postero-distal process of peduncular segment 1 of antenna 1, and the unfused urosome segment 1. However, on close inspection, his Moluccas material is seen to differ in a number of specific features such as its weaker body carination, shorter carpus of gnathopod 2, and more acute apices of the rami of uropod 3. Ledoyer's material is therefore regarded here as a species different from *A. japonicus* Nagata, and awaits formal designation as a possible new taxon.

Distributional Commentary. *Kamehatylus japonicus* has been recorded from Japanese waters mainly from Honshu and more southerly localities (see summary of pertinment literature by Ishimaru, 1994).

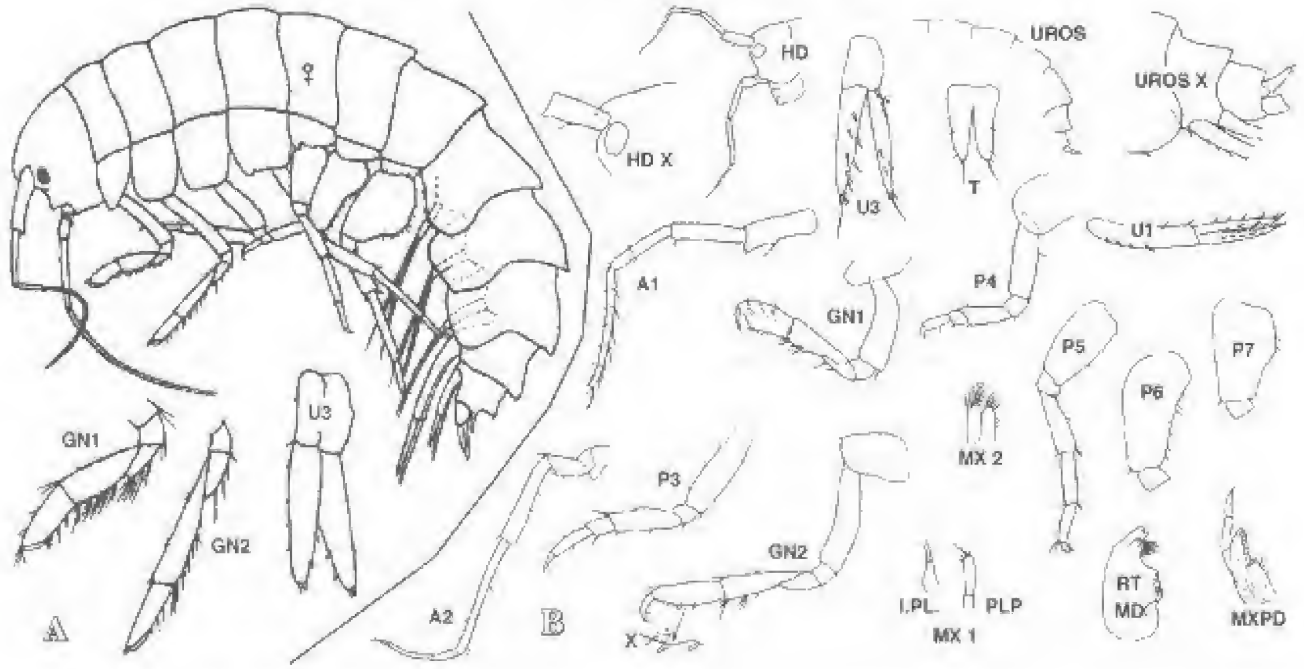

FIG. 17. ***Kamehatylux japonicus.***

A. ***K. japonicus*** **Nagata Female (3 - 5 mm) Seto Inland Sea (from Nagata, 1960)**

B. ***K. japonicus*** **Ledoyer Male (3.4 mm) Moluccas Ids. (from Ledoyer, 1979).**

DEXAMINIDAE Leach

Dexaminidae Leach 1813/14: 432.—Stebbing, 1888: 573. —Gurjanova, 1951: 788.—Lincoln, 1979: 448.—Bousfield, 1982: 212.

Dexaminidae (part) Barnard, 1969: 200.—Barnard 1970: 163.—Bellan-Santini, 1982: 277.—Barnard & Karaman, 1991: 260.

Subfamilies: Dexamininae Leach; Dexaminoculinae, new subfamily; Polycheriinae, new subfamily; Prophliantinae Nicholls.

Diagnosis: Body small, stout, compact, not compressed. Sexual dimorphism expressed in eyes, antenna, uropod 3, typically in gnathopod 1, pleopods, and telson. Peraeon segments 5-7 usually smooth above, occasionally with mid-dorsal teeth and/or dorso-lateral mucronations. Pleosome and urosome, less often posterior peraeon, armed dorsally and occasionally dorso-laterally with teeth or spines. Rostrum short. Anterior head margin rounded or acute; may be produced strongly as ocular lobe. Eyes medium to large. Antennae short (female). Antenna 2 often reduced, not longer than 1. Antenna 1, peduncular segment 2 various; accessory flagellum minute or lacking.

Lower lip, inner lobes usually strong. Mandible, molar usually strong, triturating; spine row weak; left lacinia often 4-dentate; palp lacking. Maxilla 1, palp 1-segmented (rarely 2); outer plate with 7-11 apical spines; inner plate with 0-2 apical setae. Maxilla 2, plates variously reduced, often weakly setose. Maxilliped, inner plate reduced, with apical setae only; outer plate large, broad; palp variously shortened, dactyl reduced or lacking (3-segmented).

Coxae 1-4 deep, shortest anteriorly, little (or not) indented below. Coxa 5, broad, often deep. Gnathopods, unequal, subchelate (rarely chelate); gnathopod 1 the smaller, with short carpus, propod (male) strikingly notched or excavate anteriorly. Gnathopod 2, carpus usally longer than propod.

Peraeopods 3 & 4 subequal, various, segments 5 & 6 trending to reduction in length, and subchelation. Peraeopods 5-7 subequal in length; bases typically unequally expanded, trending to linearity; segment 5 normal, occasionally shortened, segment 6 & dactyl often shortened.

Pleopods short to medium. Pleon plates 1-3, hind corners acuminate, often produced. Uropod 1, rami subequal, tips spinose. Uropod 2 much shorter than 1, outer ramus the shorter. Uropod 3, rami lanceolate (often broadly), margins variously plumose-setose, especially in male.

Telson deeply bilobate, lobes not diverging, apices subtruncate, variously armed.

Coxal gills on peraeopods 2-7 (6), variously pleated, not phylliform.

Taxonomic Commentary: As noted previously, Barnard (1970a, loc. cit) combined a number of dexaminoidean families (including Atylidae, Anatylidae, Lepechinellidae, Prophliantidae) within family Dexaminidae. His decision was based on the presence of one or more species deemed intermediate in form (often on single character states only)

KEY TO SUBFAMILIES OF DEXAMINIDAE

1. Peraeopods fundamentally simple, not subcheliform; body (esp. pleosome) variously carinated or processiferous; ..... 2.
—Peraeopods variously subcheliform; body (except urosome) smooth ..... **Polycheriinae** (p. 37)

2. Eyes enormous, located at end of interantennal lobe; coxa 3 short; antenna 2 very short in female .....
..... **Dexaminoculinae** (p. 49)
—Eyes normal, not at tip of interantennal lobe; coxa 3 normal, deep; antenna 2 little shorter than antenna 1 (female) ..... 3.

3. Body carinated on urosome; peraeopod 7, segments 4 & 5 broadened, strongly setose; gnathopod 1 propod not sexually dimorphic. ..... **Prophliantinae** (p. 51)

—Body carinated on pleon and urosome; peraeopod 7, segments 4 & 5 not broadned or heavily setose gnathopod 1, propod typcially sexually dimorphic ..... **Dexamininae** (p. 36)

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between the families in question. As noted elsewhere, this philosophy of taxonomic fusion does not recognize the Darwinian evolutionary thesis that predicts "intermediate" morphotypes existing, at one time or other, between all extant and past organisms. Thus, we agree with Ishimaru (1993) that the presence of single taxa that appear to "bridge" otherwise morphologically discontinuous higher taxa does not, alone, constitute a valid basis for merging of the pertinent higher taxa. The Barnardian classification is therefore not followed here.

In this study, numerical taxonomic analysis (p. 56) strongly supports recognition of just two family-level dexaminoidean subgroups, the Atylidae (p. 8) and the Dexaminidae (above). The analysis further supports recognition of four distinct subfamily groupings within family Dexaminidae, as listed and keyed above.

Subfamily Dexamininae (revised)
(see Fig. 2(a))

Dexamininae (part): Barnard & Karaman 1991: 260.
Dexamininae Ishimaru, 1987: 1412.

Type genus: *Dexamine* Leach, 1813/14.

Genera: *Dexamine* Leach, 1814: 432; *Dexaminella*, Schellenberg, 1928: 654; *Paradexamine*, Stebbing, 1899: 210; *Sebadexius* Ledoyer, 1984: 56; *Syndexamine* Chilton, 1914: 332.

Diagnosis: Body generally toothed or processiferous above, not strongly compressed. Rostrum medium. Eye normal. Antennae regular.

Mouthparts typical of family; Lower lip, inner lobes variously developed. Mandible, spine row weak. Maxilla 1, outer plate with 10-11 apical spines. Maxilliped, outer plate large; inner plate distinct; palp variously reduced, segments 3 & 4 shortened or vestigial.

Coxae 1-4 regular, deep, 1 smallest. Coxa 5 medium. Gnathopods typically subchelate, occasionally chelate; carpus not elongate. Gnathopod 1, propod sexually dimorphic.

Peraeopods normal, not subcheliform nor elongate; segment 5 not unusually lengthened or shortened; dactyls medium; peraeopods 5-7 subequal in length, bases dissimilar in form, variously broadened; segment 5 normal.

Pleon segments dorsally and dorso-laterally carinate. Pleon plates 2-3, hind corners variously acuminate or produced.

Telson elongate, lobes deeply separated, not diverging. Brood plates sublinear.

Taxonomic and Biogeographic Commentary: As here defined, the subfamily Dexamininae encompasses five genera and about 60 species that occur mainly in southern oceans. *Paradexamine*, with more than 40 described species, is essentially Indo-Pacific, with outliers extending to the Mediterranean, South America, and Japan. The Japanese fauna comprises ~8 described species (Ishimaru, 1994), all confined to Kyushu and the southern archipelagos; none reaches northern Honshu, and no member of the genus reaches the Pacific coast of North America. *Sebadexius* is monotypic in New Caledonia. *Syndexamine* contains 6 species, in littoral waters of New Zealand and southern Australia. *Dexaminella*, containing 3 species, is confined to the northwestern Indian Ocean and Red Sea. However, *Dexamine*, with only 3 recognized species (Barnard & Karaman, 1991) is confined to the boreal and temperate North Atlantic region, extending southward along eastern shores to the Mediterranean and Senegal, and along western shores to the Middle Atlantic States and Chesapeake Bay. Members of this subfamily have yet to be recorded authentically from the North American Pacific region and are not treated further in this study.

KEY TO WORLD GENERA OF DEXAMININAE

1. Gnathopods cheliform; maxilliped palp various, usually small to vestigial .... ***Sebadexius*** Ledoyer.

—Gnathopods subcheliform, maxilliped palp 3-4 segmented ..... 2.

2. Pleon segments distinctly carinate mid-dorsally and/or dorso-laterally, integument normal ..... 3.

—Pleon segments indistinctly or not carinated; integument often thick, heavy ..... 5.

3. Pleon segments 1-3 carinate laterally and dorsally ..... ***Paradexamine*** Stebbing

—Pleon segments carinated dorsally only ..... 4.

4. Maxilliped palp 3-segmented ..... ***Dexaminella*** Schellenberg

—Maxilliped palp 4-segmented. ..... ***Dexamine*** Leach

5. Uropods 1 & 2, inner rami reduced; peraeopod 6 massive ..... ***Delkaryle*** J. L. Barnard

—Uropods 1 & 2 normal; peraeopods 5-7 subequal, 6 not massive ..... ***Syndexamine*** J. L. Barnard

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POLYCHERIINAE, new subfamily
(See Fig. 2(c))

Dexaminidae (part) Stebbing, 1906: 514.—Barnard, 1969: 200.—Lincoln, 1979: 448.—Bellan-Santini, 1982: 212.—Barnard & Karaman, 1991: 260.

Type Genus: *Polycheria* Haswell, 1879: 345.

Generic Content: *Tritaeta* Boeck, 1876: 317.

Diagnosis: Body smooth, carinate (weakly) only on urosome. Head; rostrum very weak or absent. Anterior head lobe variously rounded. Eyes pigmented, large. Antennae 1 & 2 medium, subequal, flagella usually setose. Antenna 2, peduncular segment 4 longer than 5. Accessory flagellum lacking.

Upper lip, epistome weakly produced anteriorly. Mandibular molar, left and right sides unequal. Maxilla 1, outer plate with 7-9 apical spines. Maxilliped palp 3-, or weakly 4-segmented. Coxa 1-7 shallow, variously bifid or acute below. Gnathopods slender, dissimilar in length; weakly subchelate.

Peraeopods 3-7 delicately prehensile (subchelate, or pseudo-carpochelate); segment 4 elongate; segments 6 and/or 5 shortened. Peraeopods 5-7 subsimilar, bases sublinear, segment 7 and dactyl often reversed.

Pleopods medium, peduncle and rami not powerful. Pleon plates 1-3 , hind corners mucronate. Uropod 1, rami subequal. Uropod 2 short, rami unequal. Uropod 3, rami lanceolate, margins setose (male). Telson lobes elongate, deeply separated, marginally spinose.

Coxal gills weakly pleated, on peraeopods 2-7. Brood plates sublinear, strap-like.

Species of both *Tritaeta* and *Polycheria* are commensal mainly on sponges and colonial tunicates (Vader, 1969), clinging upside down in small pits excavated in surface test of host, and feeding in the fashion of ampeliscoideans.

Taxonomic and Distributional Commentary: The subfamily presently contains two genera, *Polycheria* and *Tritaeta*, not very closely related (p. 57), characterized by a trend to prehensility (subchelation) of peraeopods 3-7. The peraeopods of *Tritaeta* are carpochelate (fig. 28). About 20 species of *Polycheria* are known, most from tropical and warm temperate Indo-Pacific regions. Three species were previously described from temperate waters of the Asiatic Pacific coast (Bulycheva, 1952; Hirayama, 1984) and one from the Pacific coast of North America (Calman, 1898; Barnard, 1969b). *Tritaeta* contains only two species (many synonymies), both in the northeastern Atlantic and Mediterranean regions (Lincoln, 1979; Bellan-Santini, 1982).

The phyletic relationships of subfamily Polycheriinae are with the Dexamininae (p. 36; fig. 2(a)). Thus, males of the more primitive genus *Tritaeta* retain the distinctive dexaminid dorsally notched form of the propod of gnathopod 1.

Polycheria Haswell

Polycheria Haswell, 1879:345.—Stebbing, 1906 :519.—Holman & Watling, 1983: 221.—Thurston, 1974: 18.—Barnard & Karaman, 1991: 271.

Type Species. *Polycheria tenuipes* Haswell 1879.

Species (North Pacific region). *Polycheria osborni* Calman 1898; *P. carinata*, new species (p. 42); *P. mixillae*, new species (p. 44); *P. amakusaensis* Hirayama, 1984a; *P. orientalis* Hirayama 1984a; *P. japonicus* Bulycheva, 1952.

KEY TO GENERA OF SUBFAMILY POLYCHERIINAE

1. Peraeopods 3-7 pseudo-carpochelate (carpus expanding and strongly spinose distally, propod lacking palm); antennal flagella smooth; gnathopod 1, propod markedly sexually dimorphic . . . . . ***Tritaeta*** .

—Peraeopods 3-7 distinctly subchelate (propod with distal palm, carpus not expanding distally); antennal flagella strongly setose; gnathopod 1, propod not markedly sexually dimorphic. . . ***Polycheria*** (p. 37).

Diagnosis: Body stout, broadest at peraeon segments 4 & 5, mid-dorsally carinated on urosome segment 1; paired dorso-lateral ridges or small spines usually present on fused urosome segments 2 & 3. Head: rostrum very weak; anterior head lobe variously rounded; eyes large, sexually dimorphic. Antenna 1, flagella usually strongly setose.

Lower lip, inner lobes well developed. Mandible, left and right molars dissimilar in size. Maxilla 1, outer plate with 7-9 apical spines. Maxilla 2, apical setae weak. Maxilliped, palp 4-segmented.

Gnathopods very weakly subchelate. Gnathopod 1, propod not strikingly sexually dimorphic; palmar margin short to obsolescent.

Peraeopods 3-7 delicately subchelate; dactyl short, closing on short fixed finger; segment 5 short, not expanded or strongly spinose distally, variously shorter or longer than segment 6. Peraeopods 5-7, bases sublinear (may be slightly broadened in peraeopods 5 & 6).

Uropod 2, outer ramus usually the shorter. Uropod 3 (female), rami variously unequal.

Telson lobes variously fused basally, margins spinose.

Sexual dimorphism strongly expressed in eyes, antennae, pleopods, and uropod 3.

Taxonomic and Distributional Commentary: North American Pacific species differ from Asiatic Pacific species in several character states, mostly apomorphically (pp.61-62 and key below). Both groups differ from the generally more primitive species of the southern hemisphere as exemplified by the *P. antarctica* complex of species (Holman & Watling, loc. cit). Species of the North American study region are characterized by: maxilla 1, outer plate with 7 (vs. 9) apical spines; maxilliped palp short (vs. medium); coxa 1 acute (vs. rounded) below; gnathopod palmar margins distinct (vs. obsolete); peraeopods 3-7, segment 5 shorter (vs. longer) than segment 6; uropod 2, inner ramus (vs. outer ramus) the shorter; uropod 3 (female), rami subequal (vs. unequal); and telson lobes more strongly fused basally. These differences point to the need for an extensive revision of the genus, based on re-examination of species world-wide, that is beyond the scope of the present study

Polycheria osborni Calman
(Figs. 18, 19, 20)

Polycheria osborni Calman, 1898: 268, pl. 32, fig 2.—Skogsberg & Vansell, 1928: 268, figs. 1-26.—Barnard, 1975: 363, key + fig. 55.—Barnard, 1969a:103.—Barnard, 1969b: 200, fig. 25g.—Staude, 1987: 382 + key.—Barnard, 1979b: 38.—Barnard & Karaman, 1991: 272 (list).
Polycheria antarctica (Stebbing, 1875): Stebbing, 1906: 520 (part).—Alderman, 1936: 63.—Barnard, 1954a: 21.

Material Examined (CMN collections, Ottawa):
SE ALASKA: Stitka region, Slocum Pt., ELB Stn S4B4, under boulders, July 27, 1980 - 1 female ov (slide mt.).
BRITISH COLUMBIA:
Queen Charlotte Islands: none taken at outer coast sites.
North Central coast: Oval Bay, surf shore at LW, ELB Stn H10, July 12, 1964 - 1 female br. II (slide mt.), 2 other females.
S. end Vancouver I: Ucluelet, outer coast, J. Macoun coll., July, 1909, (identified initially as *P. tenuipes* Haswell) - 1 lot dried specimens.
Barkley Sd. region, ELB Stns, 1975-76:
Taylor I., Trevor Ch.annel, ELB Stn. P5b c. on ascidians and sponges, LW, July 25, 1975 - 1 female br II (4.5 mm) (slide mt); 1 female ov (5.2 mm) (slide mt.); 2 female ov. (4.5, 4.8 mm) (slide mts.); 1 male many specimens.
Kirby Pt., Diana I., ELB Stn. P17d, on sponges and ytunicates from rocky walls of surge channels, LW and subtidal, Aug. 6, 1975 - 1 female ov. (5.8 mm) (slide mt - fig'd specimen); 1 male (3.7 mm) (slide mt.- fig'd specimen), 2 subad. males (4.3, 4.5 mm); 1 subad. female (4.2 mm) (slide mt.); several other specimens.
Bordelais Islets, mouth of Trevor Ch.., ELB Stn. P20c, from sponges and tunicates on rocky walls of surge channels, Aug. 9, 1975 - 1 female ov. (6.0 mm) (slide mt.)2 subad. males (5.0 mm, 3.8 mm)
Edward King I.,Taylor I.,ELB Stn B28a, under boulders at LW, July 10, 1976 - 1 female ov. (5.0 mm) (slide mt.); 1 female br. II (5.3 mm) (slide mt.); several other specimens, mostly subad. females.
WASHINGTON-OREGON: No specimens were found in tcollections from apparently suitable habitats at localities along the outer coast (see Bousfield & Jarrett, 1981).

Diagnosis. Female ov. (5.8 mm): Urosome 1, mid-dorsal carina low, weakly toothed behind. Eye medium, covering anterior half of head, golden brown in colour in fresh material. Anterior head lobe broadly rounded. Antenna 1, segment 3 short; flagellum 20+ segmented, moderately setose. Antenna 2, flagellum 18-segmented.

Mandible, spine row with 2-3 short blades. Maxilla 1, inner plate with 1-2 apical setae; outer plate with 7 slender apical spines; palp short. Maxilla 2, plates small weakly

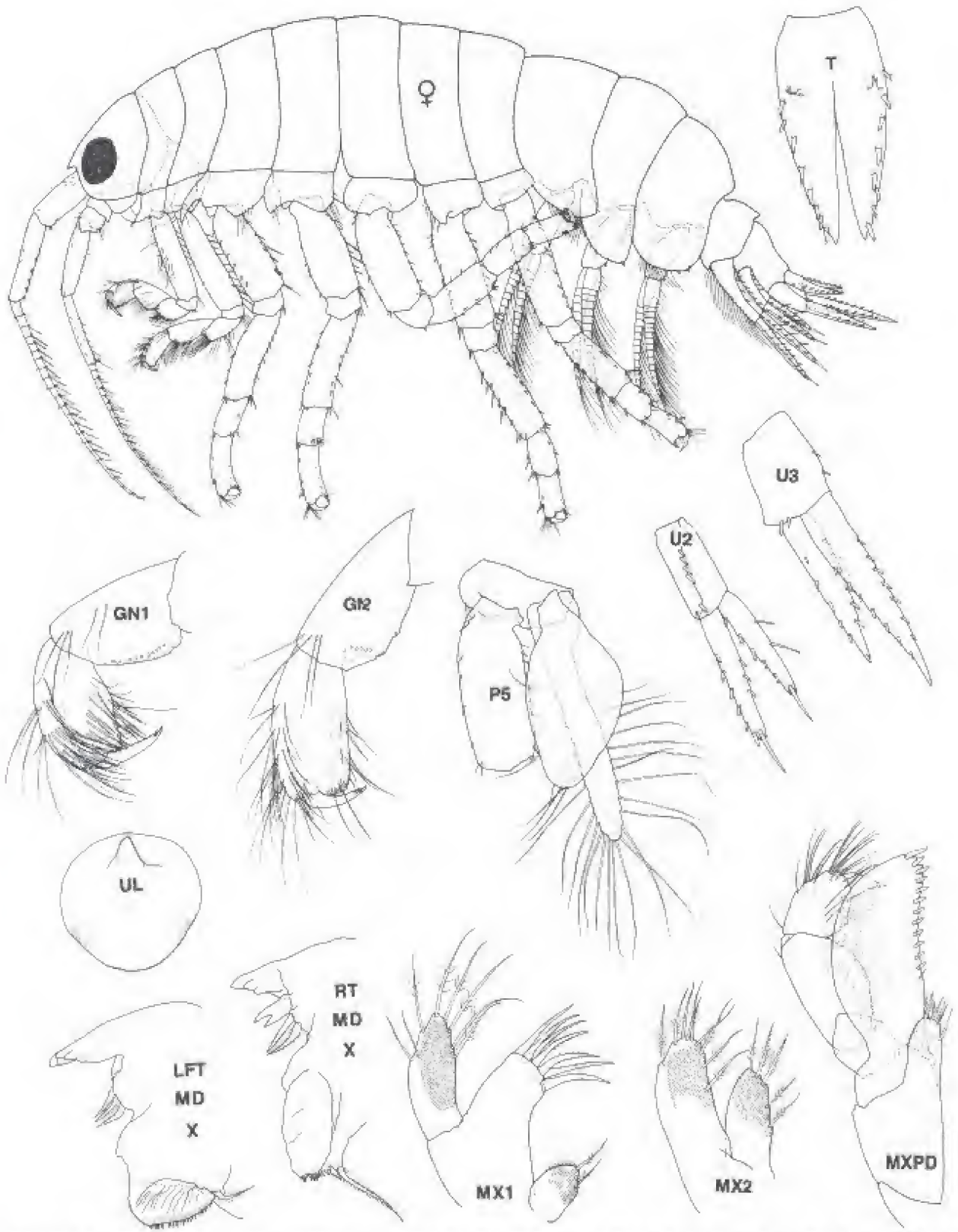


FIG. 18. ***Polycheria osborni*** **Calman. Kirby Pt., Diana I., Barkley Sound. Female ov (5.8 mm).**

plumose-setose. Maxilliped, outer plate with 12 inner marginal spines; palp shorter, dactyl thick.

Coxa 1 sharply acute anteriorly; coxa 3, anterior process elongate, length > 3X basal width. Gnathopod 1, carpus and propod subequal in length, carpus proximally deepest; dactyl slender, projecting > 50% of its length beyond short palm. Gnathopod 2, propod more slender, shorter than carpus, palm short but distinct, slightly exceeded by closed dactyl.

Peraeopods 5-7, segment 5 shorter than segment 6. Peraeopods 3 & 4, basis slightly broader than distal segments. Peraeopods 5-7, bases sublinear, not broadened; segment 6 shorter than in peraeopods 3 & 4.

KEY TO NORTH PACIFIC SPECIES OF POLYCHERIA

1. Urosome segment 1 posteriorly extended, partially concealing fused urosome segments 2 & 3; peraeo-pods 3-7, segment 5 not shorter than 6; uropod 2, outer ramus shorter than inner; maxilla 1, outer plates with 9 apical spines; maxilla 2, inner plate, inner margin setose (Asiatic Pacific) . . . . 2.

—Urosome segment 1 not extended posteriorly, based of urosome segments 2 & 3 open; peraeopods 3-7, segment 5 shorter than 6; uropod 2, inner ramus the shorter; maxilla 1, outer plate with 7 apical spines; maxilla 2, inner plate with weak apical setae only (North American Pacific). .4.

2. Gnathopods 1 & 2 subchelate, palm distinct; peraeopod 5, basis expanded, length < 2X width . . . . ***P. japonicus*** (p. 44)

—Gnathopods 1 & 2 nearly simple, propod palmar margins very short or obsolete; peraeopod 5, basis sub-linear, length > 2X width . . . . 3.

3. Peraeopods 6 & 7, segment 6 distinctly shorter than segment 5; pleon plate 1, hind corner rounded . . . . ***P. amakusaensis*** (p. 46)

—Peraeopods 6 & 7, segments 5 & 6 subequal in length; pleon plate 1, hind corner acuminate . . . . ***P. orientalis*** (p.47)

4. Eye medium, covering anterior half of head; gnathopod 1, dactyl long, extending >50% of its length beyond palm; coxa 3, anterior process strong, length >3 X basal width; telson, lateral margins with 7-8 spines . . . . ***P. osborni*** (p. 38)

—Eye large, covering 3/4 width of head; gnathopod 1, dactyl medium, extending< 50% of its length beyond palm; coxa 3, anterior process medium, length 2-3 X basal width; telson, lateral margins with 5-6 spines . . . . 5.

5. Antenna 1 strongly setose posteriorly on flagellum and peduncular segment 2; gnathopod 1, propod distinctly shorter than carpus, dactyl basally broad, thick; coxa 3, anterior process medium, length > 2X basal width . . . . ***P. carinata*** (p. 42)

—Antenna 1, flagellum and peduncular segment 2 moderately to weakly setose posteriorly; gnathopod 1; propod and carpus subequal in length, dactyl basally slender; coxa 3, anterior process short, length < 2X basal width . . . . ***P. mixillae*** (p. 44)

Pleopods medium, rami ~12-segmented; pleon plates 1-3, hind corners squarish or obtuse. Uropods 1, peduncle, anterior (outer) margin richly setose, apical spines of rami elongate. Uropod 2, inner ramus the short, inner margin with 2 medial long spines. Uropod 3, outer margin shorter, outer margin 4-5 spinose.

Telson, lobes slender, basal 1/4 fused, margins with 7-8 short spines, apices acute.

Male. (5.0 mm): Eye very large, broadly reverse-reniform, covering 5/6 head width. Antennae 2 longer than antenna 1, brush setae present on the posterior margin of peduncular segment 2, antenna 1, and the anterior margin of peduncular segment 3 & 4 of antenna 2; flagellum lacking feeding setae.

Gnathopod 1, propod more slender and palm virtually lacking; gnathopod 2, propod longer and more slender, and palm very much shorter, than in female.

Pleopods, peduncles strong, massive, nearly 2X longer than in female; split-tipped clothespin spines on 5-6 proximal segments of inner ramus. Urosome, mid-dorsal carina elevated, not mucronate behind; fused urosome segments 2 & 3 with mid-dorsal notch. Uropod 2, inner margin of peduncle with a few plumose setae; inner margin of inner ramus with 3 slender spines. Uropod 3, outer ramus slightly the shorter, outer margin with a few spines, all other margins (of both rami) heavily plumose-setose.

Telson relatively shorter, broadest medially, lobes more deeply separated, margins less spinose than in female.

Distribution: Commonly encountered in tests of *Amaroucium* (Skogsberg & Vansell, 1928), from Central California north to British Columbia and southeastern Alaska; questionably southward to the Gulf of California and Galapagos. The probability is high that *P. osborni* is a complex of sibling species over such a broad geographical range.

Taxonomic Commentary: The female of the present material compares closely with the original figures of Calman (fig. 19, above) based on material from Puget Sound. Particularly diagnostic of the species is the small palm of gnathopod 1, greatly exceeded by the dactyl. The species *Polycheria antarctica* (Stebbing, 1888), described originally from sponges in the Antarctic and ANZAC regions, is not a true synonym of *P. osborni*, but is a distinctive species that exhibits generally more plesiomorphic characters states (p. 49, fig. 25).

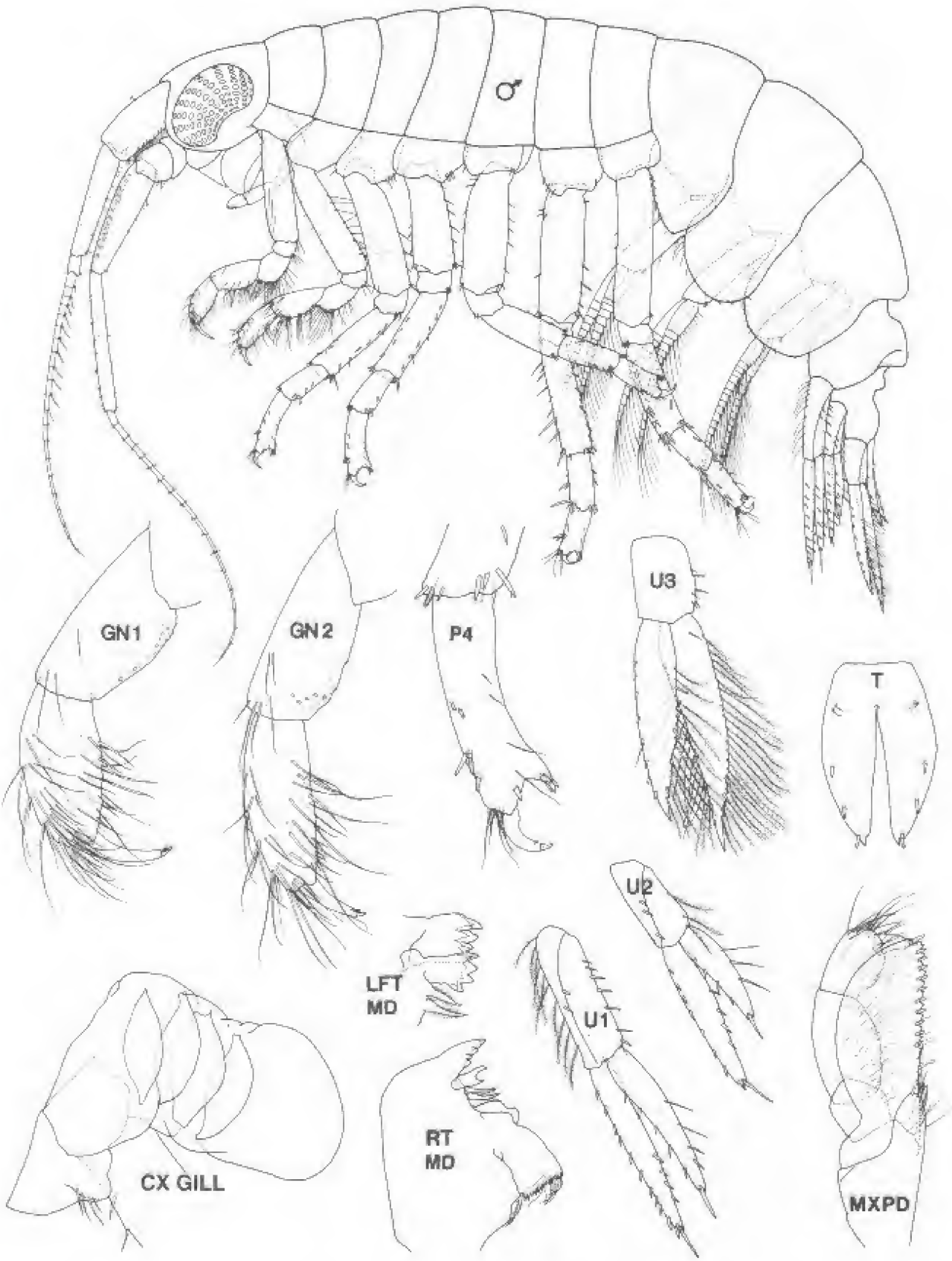


FIG. 19. ***Polycheria osborni*** **Calman. Kirby Pt, Diana I, Barkley Sound. Male (3.7 mm)**

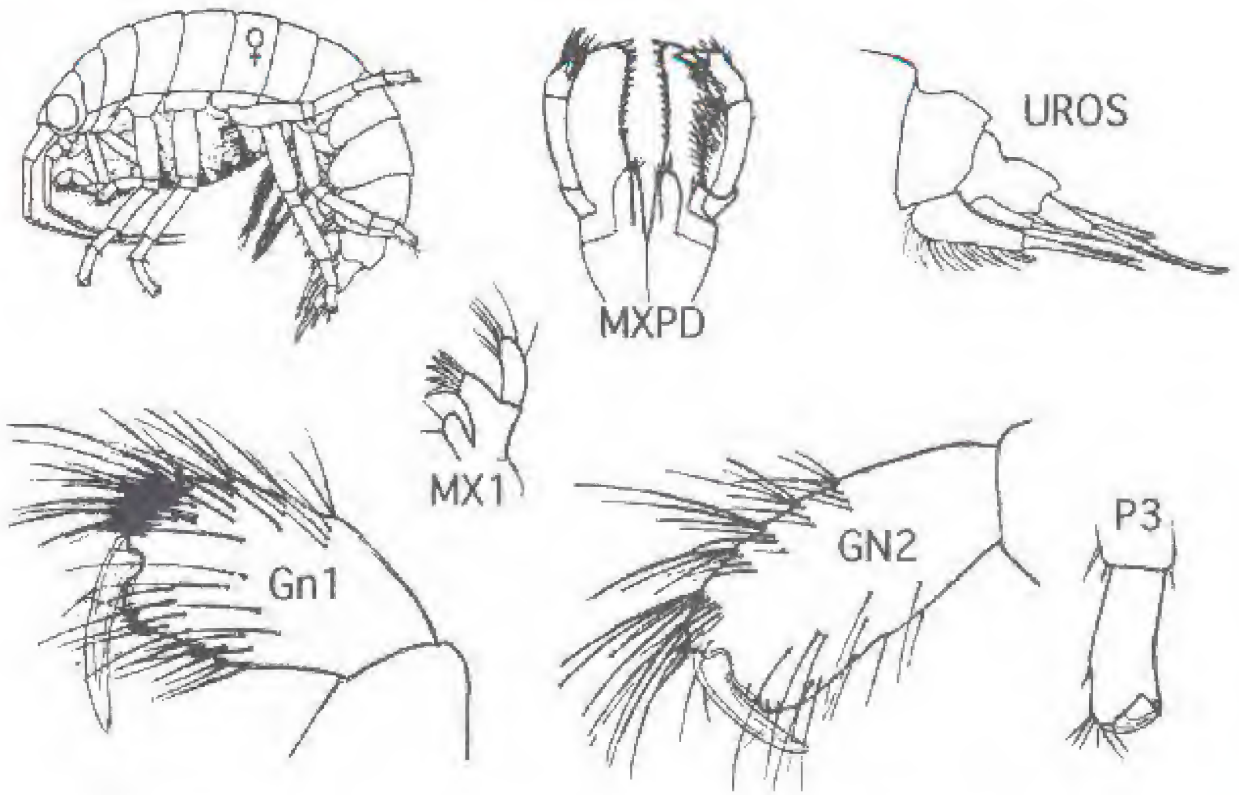


FIG. 20. ***Polycheria osborni*** **Calman. Female ov. (7.0 mm) Puget Sound (modified from Calman, 1898)**

Polycheria carinata, new species
(Fig. 21)

Material Examined:
BRITISH COLUMBIA:
Mainland coast: Athlone I., ELB Stn. H53, under boulders, LW, Aug. 7, 1964 - 1 female ov (5.8 mm) Paratype (slide mt.) CMN Cat. No. NMCC1994-0392; 2 additional females.
S. end Vancouver I.: Taylor I., Trevor Channel, ELB Stn. P5c, from ascidians and sponges beneath boulders, LW, July 25, 1975 - 1 female br. II (4.0 mm) (slide mt.).
McCaulay Pt., Victoria, B. C., GW O'Connel dive coll., Aug. 26, 1976 - 1 female ov. (4.0 mm) Holotype (slide mt.) CMN Cat. No. NMCC1994-0390; 6 female, 1 subadult male specimens, Paratypes. CMN Cat. No. NMCC1994-0391.

Diagnosis. Female br. II (4.0 mm). Urosome segment 1 and fused segments 2 & 3 dorsally and dorso-laterally sharply ridged or keeled, not acuminate behind. Eye large, red or black (in alcohol), covering anterior 3/4 of head width. Anterior head lobe very broadly rounded. Antennae subequal, flagella and distal peduncular segments richly armed with longish food-gathering (feeding) setae.

Mouthparts typical of N. American generic subgroup. Maxilla 1, outer plate, apical spines relatively long, palp short. Maxilla 2, outer plate, apex subtruncate, weakly setose. Maxilliped, palp very short, dactyl small; outer plate with 10 inner marginal spines.

Coxa 1 acutely produced anteriorly; coxa 3 moderately produced, length> 2X basal width; coxa 4 blunt, rounded in front. Gnathopod 1, propod relatively short and deep, lower margin with several stiff setae; palm very short, dactyl normal slender (in paratype), large, heavy, basally thick or broad, apparently abnormally developed in holotype. Gnathopod 2 more slender, carpus and propod subequal in length, palm very short.

Peraeopods 3-7, segment 5 shorter than segment 6. Peraeopods 3 & 4, basis relatively heavy, broader than distal segments. Peraeopods 5 - 7, bases narrow, slightly broadened in 5; segment 6 with relatively strong antero-distal cluster of setae.

Pleopods medium, rami 12-14 segmented. Pleon plates 2-3, hind corners squarish, not acuminate; pleon 3 setose below. Uropod 1, peduncular anteriorly line with setae; rami elsely subequal apical spines not elongate. Uropod 2, rami much longer than peduncle, apical spines short. Uropod 3, outer ramus slender, length about 80% inner ramus, outer margin with 2-3 short spines, othe rmargins spinose.

Telson lobes narrowing distally, fused in basal 1/4, outer margins with 5-6 small spines.

Distribution: Known from Southern Vancouver I, north to Athlone I central B. C. coast. Host unknown.

Taxonomic Commentary:. The species is closest to *P. mixillae* in most character states, but is distinguished mainly by features of the key (p. 40).

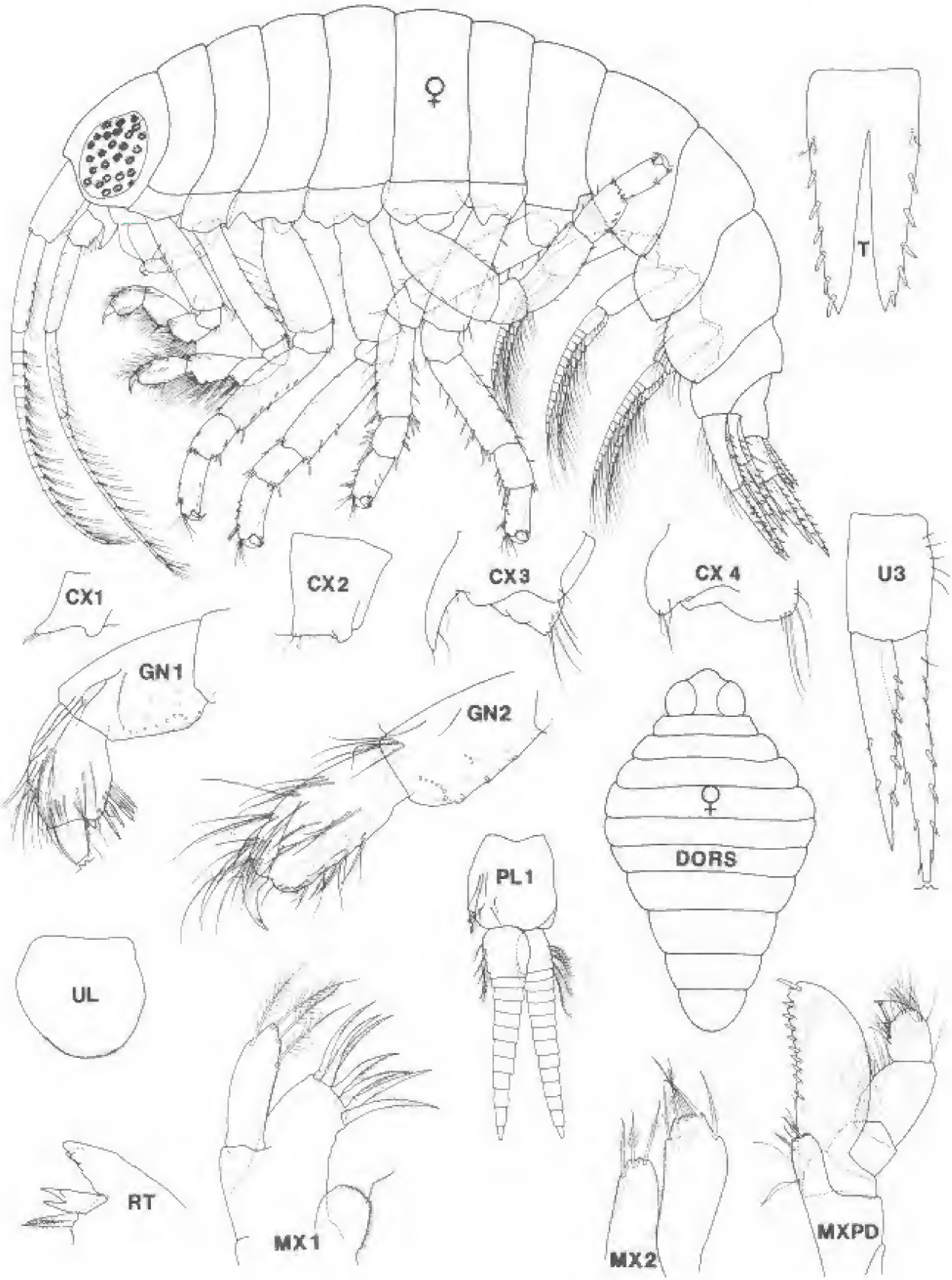


FIG. 21. *Polycheria carinata,* **new species. McCaulay Point, B. C. Female Br. II (4.0 mm).**

Polycheria mixillae, new species
(Fig. 22)

Material Examined (CMN collections, Ottawa):
BRITISH COLUMBIA:
S. end Vancouver I.: Diana I., Kirby Pt., R. Anderson coll., from sponge *(Mixilla incrustans)*, June 25, 1976 - 1 female br II (4.0 mm) Holotype (slide mt.), CMN Cat. No. NMCC1994-0393; 9 other females, Paratypes, CMN Cat. No. NMCC1994-0395.
Bordelais Islets, entrance to Trevor Channel, ELB Stn. P20c, LW, in sponges and tunicates (undet.) collected from rocky walls of surge channels, Aug. 9, 1975 - 1 female br. II (4.0 mm)(slide mt.).

Diagnosis. Female ov. (5.0 mm). Urosome 1, dorsal carina low, not produced posteriorly. Urosome segments 2 & 3, carinae or ridges inconspicuous. Head relatively shallow, anterior head lobe strongly rounded. Eyes very large, ovate, weakly faceted, covering anterior 3/4 of head. Antennae subequal, slender. Antenna 1, segment 2 postero-distally with longish setae; segment 3 short, flagellum ~16-segmented, moderately strongly setose, setae long. Antenna 2, flagellum 3-segmented.

Lower lip broad, inner lobes large. Mandible, spine row with 2-3 blades. Maxilla 1, inner plate with 1 apical seta; outer plate with 7 slender apical spines; palp short. Maxilla 2, inner plate small, weakly setose apically; outer plate, apex subacute. Maxilliped palp short, dactyl stout; outer plate, inner margin with 7-8 weak masticatory spines.

Coxa 1, anterior process short, with 2 apical setae. Coxa 3, anterior process relatively short, with single apical seta; coxa 4, anterior lobe rounded. Gnathopod 1, basis lacking hind marginal setae; propod shorter than carpus, lower margin distally with 5-6 stout setae; palm short, exceeded by nearly 50% of slender dactyl when closed. Gnathopod 2 slender, propod much shorter than carpus, palm distinct, barely exceeded by simple dactyl.

Peraeopods 5-7, segment 5 shorter (or not longer) than segment 6. Peraeopods 3 & 4, basis heavy, broader than distal segments. Peraeopods 5-7, bases sublinear, very slightly broader in peraeopods 5 & 6; segment 5 shorter than in peraeopods 3 & 4; coxa 7 produced posteriorly, subacute.

Pleopods medium, rami ~13-15 segmented. Pleon plates 1-3 broad, hind corners squarish or obtuse. Uropod 1, peduncle, anterior margin strongly setose; rami slender, subequal, apical spines elongate. Uropod 2, rami longer than peduncle, inner ramus short, inner margin with 2 longish slender spines. Uropod 3, inner ramus with inner marginal spines and a few setae; outer ramus shorter, outer margin lined distally with 3-4 short spines.

Telson lobes basally one-fourth fused, narrowing distally, margins distally with 4-6 short spines, apices acute.

Coxal gills large, sac-like, weakly pleated, on peraeopods 2-5, smaller on peraeopods 6 & 7. Brood plates sublinear.

Mature male undescribed.

Etymology: The root name refers to the genus of sponges, *Mixilla*, with which the amphipod species appears to be commensally associated.

Distribution: Known only from the Barkley Sound region of Vancouver I. Commensal on Demospongia *(Mixilla incrustans)*

Taxonomic Commentary: The species is closely related to *P. carinata* within the North American taxonomic complex of species. *P. mixillae* is distinguished from it by characters provided in the key (p. 40), by the somewhat less strongly reduced palp of the maxilliped, and by the more setose inner ramus of uropod 3.

WESTERN PACIFIC SPECIES OF *POLYCHERIA*.

The principal character states of the three species of *Polycheria*, previously described and figured from the western Pacific region, are here summarized for inclusion in analysis of relationships of the North American Pacific fauna (see also Table III, and Fig. 31).

Polycheria japonica Bulycheva
(Fig. 23)

Polycheria japonica Bulycheva, 1952: 233.—Barnard & Karaman, 1991: 272.

Taxonomic commentary: The original description and figures were based on a male specimen, but pertinent non sexual character states are here summarized:

Fused urosome segments 2 & 3 bearing small dorsal spines and paired lateral ridges, antero-laterally masked by posterior projection of urosome segment 1. Antenna 1, peduncular segment 3 longer than adjacent flagellar segments.
Mandible, left and right molars unequally reduced. Maxilla 1, outer plate with 9 apical spines; palp large. Maxilla 2, inner plate strongly setose. Maxilliped, palp medium, slightly exceeding tall outer plate.

Coxae 1 & 2 anteriorly rounded below. Coxa 3 lacking anterior process. Gnathopod 1, propod relatively short, deep; palm large, not exceeded by dactyl. Gnathopod 2, propod slender, subequal in length to carpus, palm distinct.

Peraeopods 3-7, segment 5 larger (not smaller) than segment 6; bases stout, somewhat broadened.

Pleon plates 2-3, hind corners acuminate. Uropod 2, outer ramus the shorter. Uropod 3, outer ramus the shorter, outer margin spinose. Telson lobes narrowing distally, fused in basal one-sixth, margins weakly spinose.

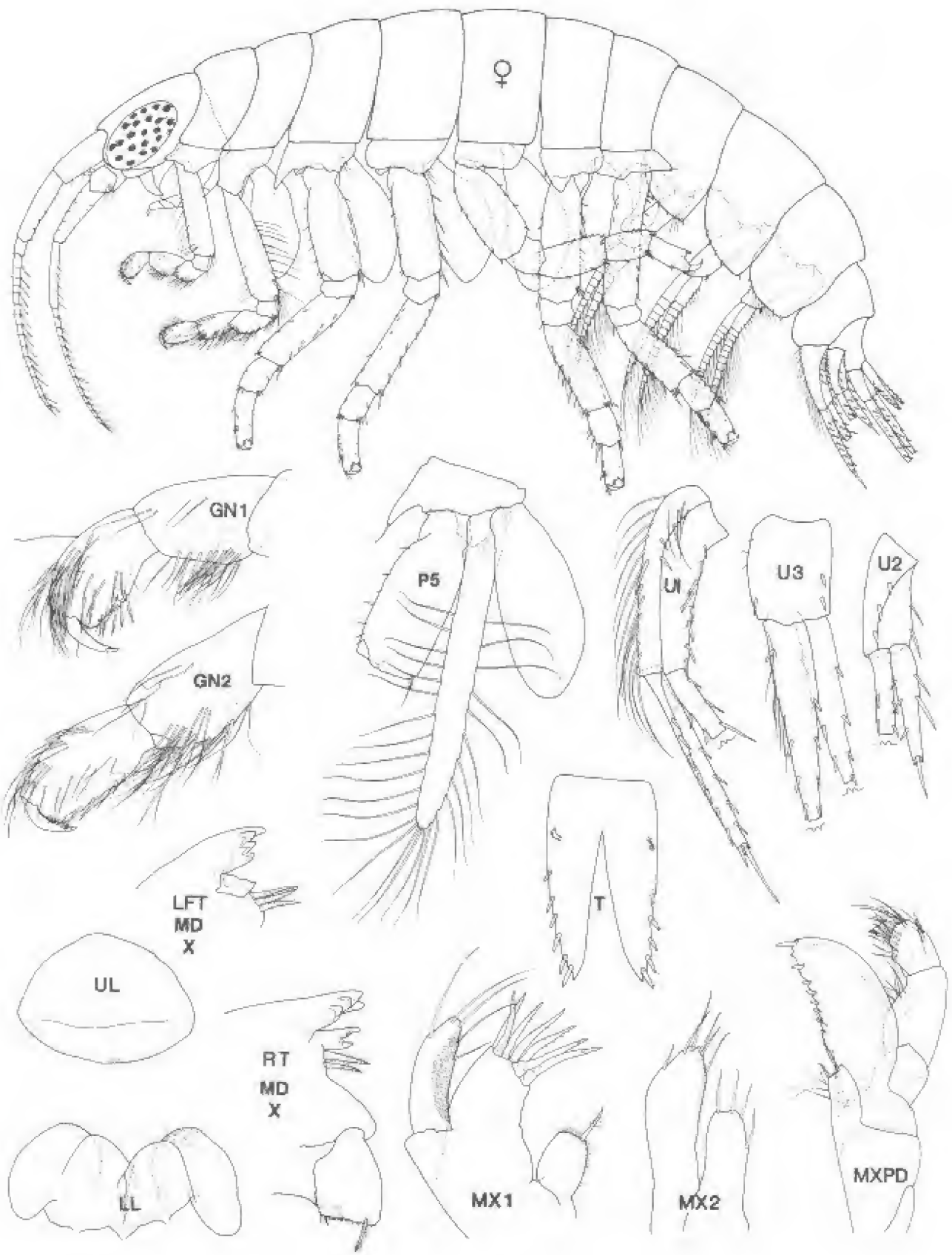


FIG. 22. ***Polycheria mixillae,*** **new species. Diana I., Barkley Sound. Female ov (5.0 mm)**

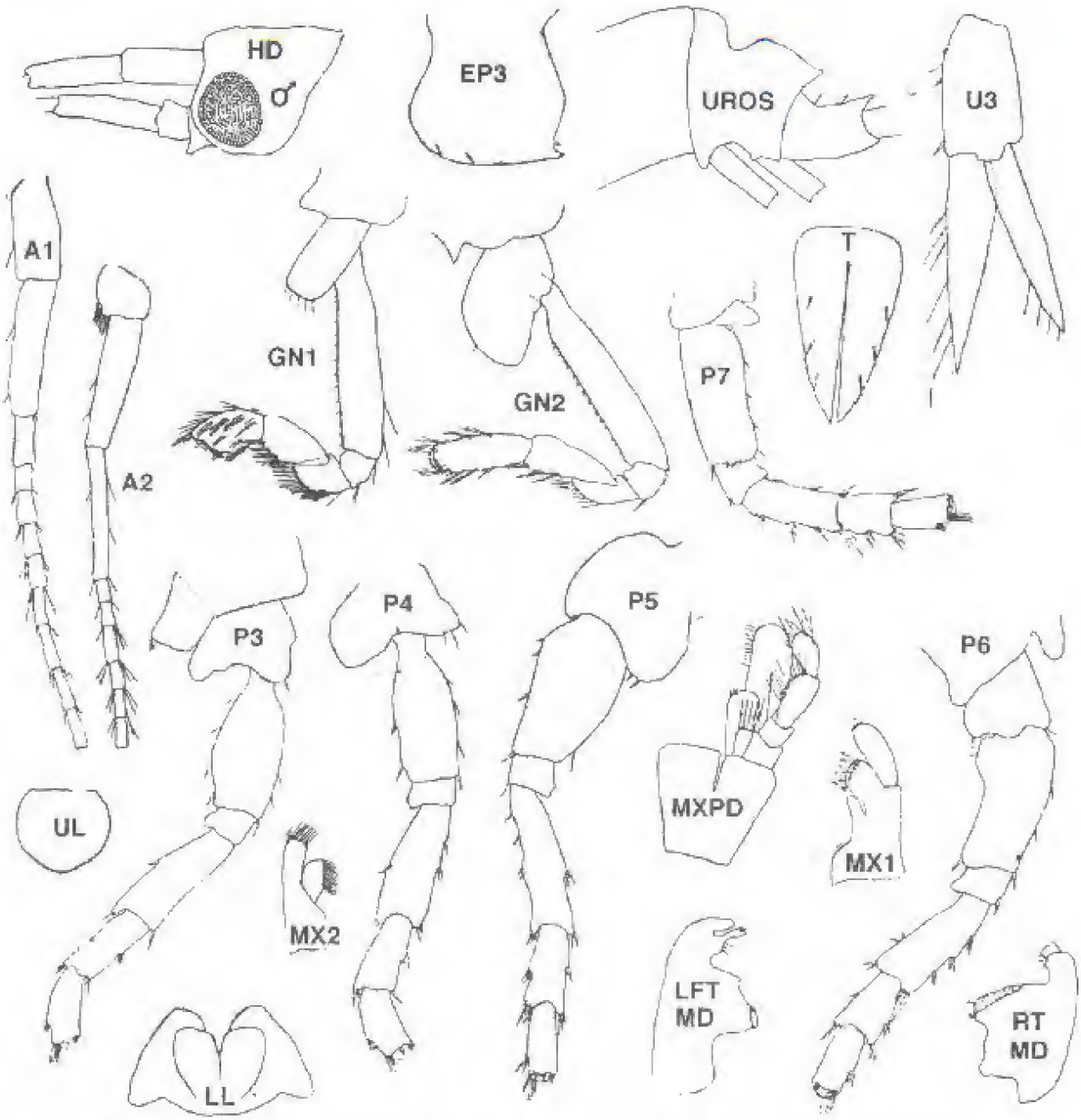


FIG. 23. ***Polycheria japonica*** **Bulycheva. Male (5.0 mm). Peter-the-Great Bay.**

Polycheria amakusaensis Hirayama
(Fig. 24B)

Polycheria amakusaensis Hirayama, 1984a: 194, figs. 106-108.—Barnard & Karaman, 1991: 271.—Ishimaru, 1994: 43.

Taxonomic Commentary: Hirayama's descriptions and figures (loc. cit) pertain essentially to a male specimen, but pertinent non-sexual character states are here summarized:

Fused urosome segments 1 & 2 with paired lateral ridges, basally masked by posterior projection of urosome segment 1. Antenna 1, peduncular segment 3 longer than adjacent flagellar segment; flagellar setation probably as in *P. orientalis*.

Mandible, left and right molars unequally reduced. Maxilla 1, outer plate with 9 apical spines; palp long. Maxilla 2, inner plate with strong medial setae. Maxilliped palp medium, about as tall as outer plate.

Coxae 1 & 2 rounded below. Coxa 3 rounded anteriorly. Gnathopod 1, propod subovate, lacking palm; dactyl short, strongly curved. Gnathopod 2, propod slender, shorter than carpus, palm and dactyl short.

Peraeopods 3-7, segment 5 larger (not smaller) than segment 6; bases little broader than distal segments except in peraeopod 5.

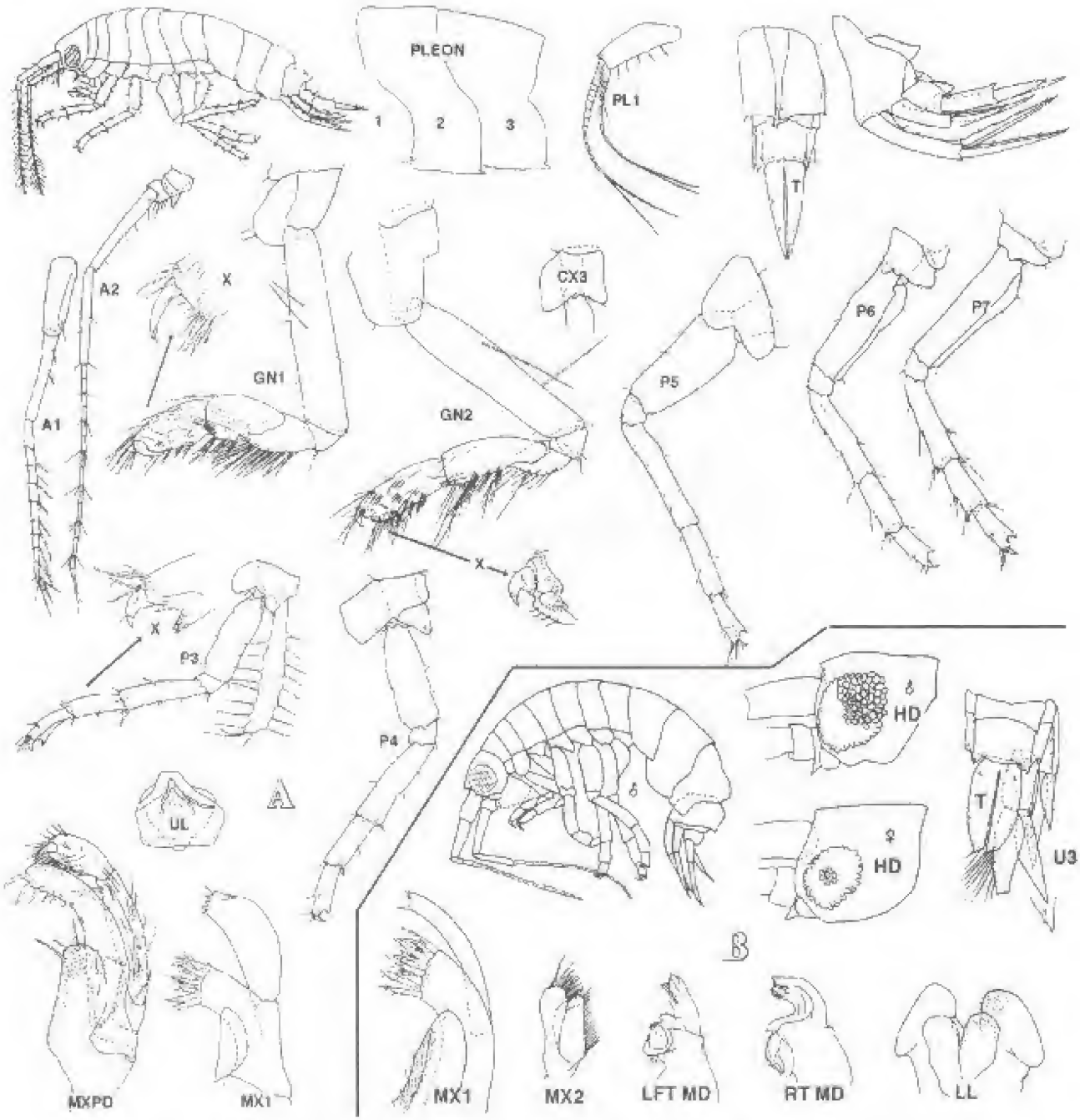


FIG. 24. ***Polycheria*** **species, West Kyushu, Japan. (after Hirayama, 1984). A.** ***P. orientalis*** **Female (4.5 mm). B.** ***P. amakusaensis*** **Male (4.5 mm).**

Pleon plates 2-3, hind corners acuminate. Uropod 1, rami subequal. Uropod 2, outer ramus the shorter. Uropod 3, outer ramus slightly the shorter, outer margin weakly spinose. Telson lobes of female not described (probably as in *P. orientalis*).

Polycheria orientalis Hirayama (revised status)
(Fig. 24A)

Polycheria atolli orientalis Hirayama 1984a: 187, figs. 101, 103-105.—Barnard & Karaman, 1991: 272.—Ishimaru, 1994: 43.

Taxonomic Commentary: The pertinent taxonomic character states of Hirayama's description and figures, based on a female specimen, are summarized here:

Fused urosome segments 1 & 2 (one illustration shows an inter-segmental line!) with small spines and paired lateral ridges, based partly masked by posterior projection of urosome 1. Antenna 1, peduncular segment 3 longer than adjacent flagellar segment; flagellum richly armed with feeding setae.

Mandible, left and right molars not shown, probably as in *P. amakusaensis*. Maxilla 1, outer plate with 9 apical spines; palp large. Maxilla 2, inner plate marginally setose.

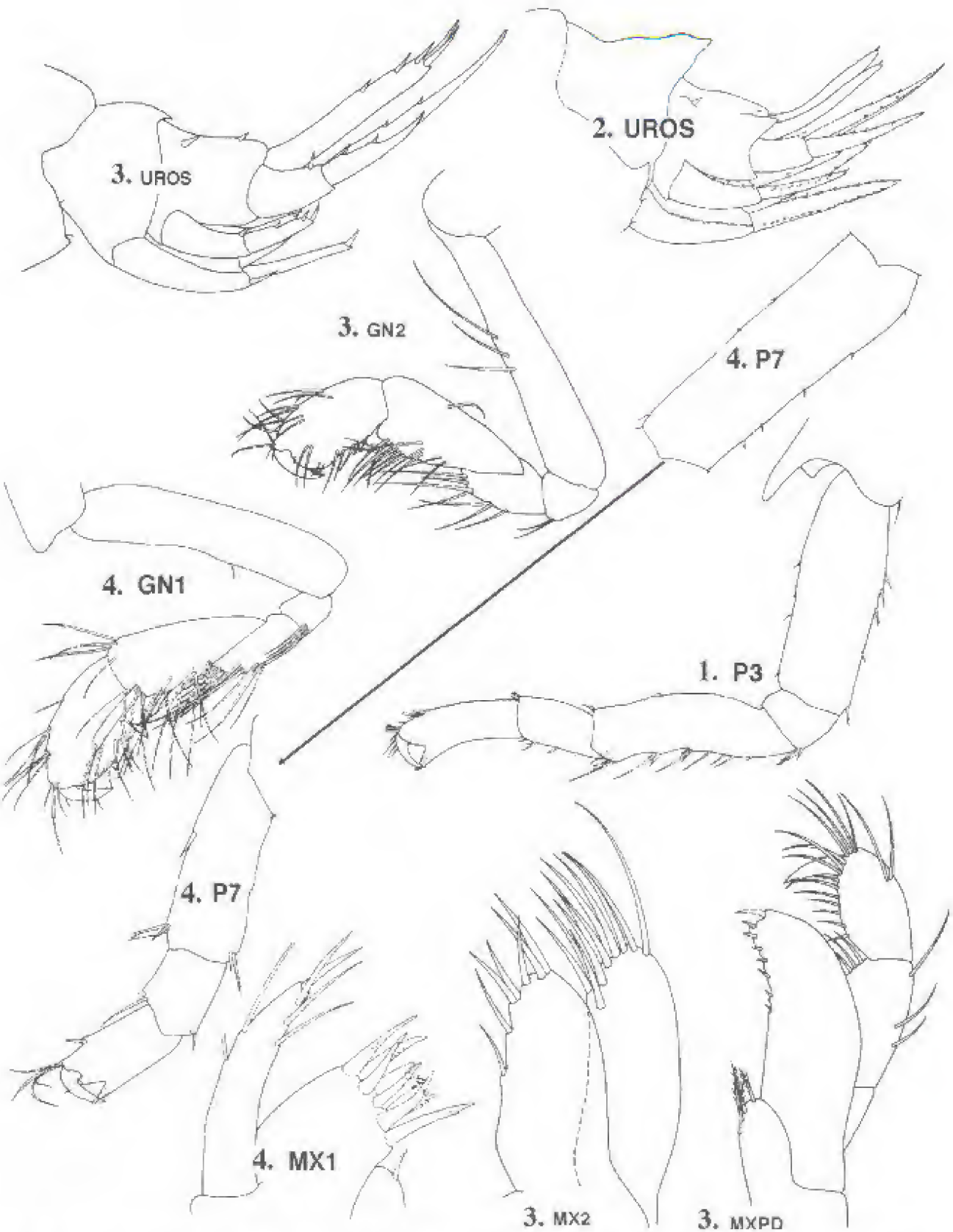


FIG. 25. ***Polycheria antarctica*** **species complex 1.** ***acanthopoda*** **Thurston. 2.** ***dentata*** **Schell. 3.** ***gracilipes*** **Schell. 4.** ***nudus*** **Holman & Watling.**
(modified from Holman & Watling, 1983)

Maxilliped, palp slightly exceeding tall outer plate.

Coxae 1, 2, & 3 rounded antero-ventrally. Gnathopod 1, propod and carpus subequal; palm short, barely exceeded by dactyl. Gnathopod 2, propod shorter than carpus; palm small; dactyl very small, hook-like.

Peraeopods 3-7, segment 5 little shortened, distinctly longer than segment 6; bases sublinear but broader than in *P. amakusaensis*.

Pleon plate 2-3, hind corners acuminate. Uropod 1, rami subequal. Uropod 2, outer ramus the shorter. Uropod 3, outer ramus the shorter, outer margin weakly spinose. Telson lobes long, narrowing distally, fused in basal one-eighth, margins weakly spinose.

EXTRALIMITAL SPECIES

Polycheria antarctica (Stebbing)
(Fig. 25.)

Dexamine antarctica Stebbing 1875: 184.
Tritaeta antarctica Stebbing 1888: 451
Polycheria antarctica Stebbing, 1906: 520, figs. 90, 91.—Schellenberg, 1931: 214.—Thurston, 1974: 18.—Holman & Watling, 1983: 221, figs. 6-9 (including forms *acanthopoda* Thurston; *dentata* Schellenberg; *gracilipes* Schellenberg; *nudus* (Holman & Watling).—Barnard & Karaman, 1991: 271.

Taxonomic Commentary: Pertinent taxonomic character states from an assemblage of "formae" of *P. antarctica* (cf. Holman and Watling, 1983), restored as distinct species of the *antarctica* complex by Barnard & Karaman (loc. cit.), provide broader perspective to the analysis of North Pacific species relationships (p. 61, fig. 31).

Fused urosome segments 2 & 3 dorsally with 4 spines, and paired lateral ridges. Urosome 1 with low dorsal carina, not produced postero-laterally to conceal base of urosome 2. Antenna 1, peduncular segment 3 slightly longer than adjacent flagellar segment; antennal flagella setose.

Mandibular molars probably unequally reduced (cf. illustration of Stebbing, 1906). Maxilla 1, outer plate with 9 apical spines; palp medium, slightly shorter than outer plate. Maxilla 2, inner plate with sparse inner marginal setae. Maxilliped, palp little reduced, exceeding tall outer plate.

Coxae 1 & 2 rounded below. Coxa 3 with strong antero-ventral process. Gnathopod 1, propod slender shorter than carpus; palm medium, little exceeded by dactyl. Gnathopod 2, propod shorter than carpus, palm relatively large, not exceeded by dactyl.

Peraeopod 3-7, segment 5 reduced, shorter than 6; bases sublinear, little broader than distal segments.

Pleon plate 2 & 3, hind corners weakly acuminate. Uropod 1, inner ramus distinctly the shorter. Uropod 2, rami subequal. Uropod 3, outer ramus much the shorter, outer margin nearly bare. Telson, lobes elongate, separated nearly to base, margins distally bare or weakly spinose, apices each with spine.

DEXAMINOCULINAE, new subfamily
(see Fig. 2(b):26)

Incertae sedis, Barnard, 1969a: 480, fig. 173a.
Dexaminidae (part) Ledoyer, 1979: 65.—Lowry, 1981: 190.
Prophliantinae Barnard & Karaman, 1991: 273 (key) (part).

Type genus: *Dexaminoculus* Lowry 1981: 191. *(Sphaerophthalmus* Spandl, 1923).

Diagnosis: An Indo-Pacific monotypic group, of unusual morphology, about which little is known except for the studies of Lowry (loc. cit.).

Body smooth or weakly toothed on peraeon. Pleon segments and urosome 1, each with mid-dorsal carination and postero-lateral marginal teeth or cusps. Urosome segments 1 & 2 ridged mid-dorsally and mid-laterally. Rostrum medium, slender. Eye large, on produced lateral cephalic lobe. Antenna 1 elongate (both sexes), accessory flagellum vestigial. Antenna 2 very short, flagellum vestigial (female); elongate, with peduncular brush setae (male).

Mouthparts nearly regularly dexaminid. Mandibular molar triturative, blades few. Maxilla 1, outer plate with 11 apical spines. Maxilla 2, plates not slenderized. Maxilliped, inner plate small; palp 3-segmented (female).

Coxae 1-4 medium, unequal, 3 smallest (allowing for respiratory current exit?), lower margins crenulate and/or setose. Coxa 5 large, anterolobate. Gnathopods dissimilar in size and form, distinctly subchelate. Gnathopod 1, propod sexually dimorphic, somewhat as in the typical dexaminid, but with the dorsal notch reduced to a shallow depression, and the palm deeply excavate, rather than convex. Peraeopods 3-7 slender, regular (not subchelate); peraeopod 5 slightly the longest. Peraeopods 5-7, bases dissimilar, variously broadened and lobate below; segment 5 not shortened; dactyls slender.

Pleon plates large; pleon plates 2 & 3, postero-lateral margin toothed, hind corners acuminated, hooked. Pleopods not described. Uropods 1 & 2 large, regular; uropod 2 short. Uropod 3, rami large, broadly lanceolate. Telson large, elongate, lobes not diverging apically.

Coxal gills and brood plates not described.

Species: *Dexaminoculus acutipes* Ledoyer, 1979 (Madagascar); *D. cavimanus* Ledoyer, 1982 (Madagascar); and *D. groebbeni* (Spandl, 1923) (Lowry, 1981) (Madagascar to Australia).

Taxonomic and Biogeographic Commentary: The genus *Dexaminoculus* was first described as *Sphaerophthalmus* by Spandl (1923) and placed in taxonomic category incerta sedis by Barnard (1969a). Two further species were described, both from Madagascar, by Ledoyer (1979, 1982). The genus is narrowly Indo-Pacific, not yet known from Japan and the North Pacific region, but might be anticipated at the northern limit of coralline substrata.

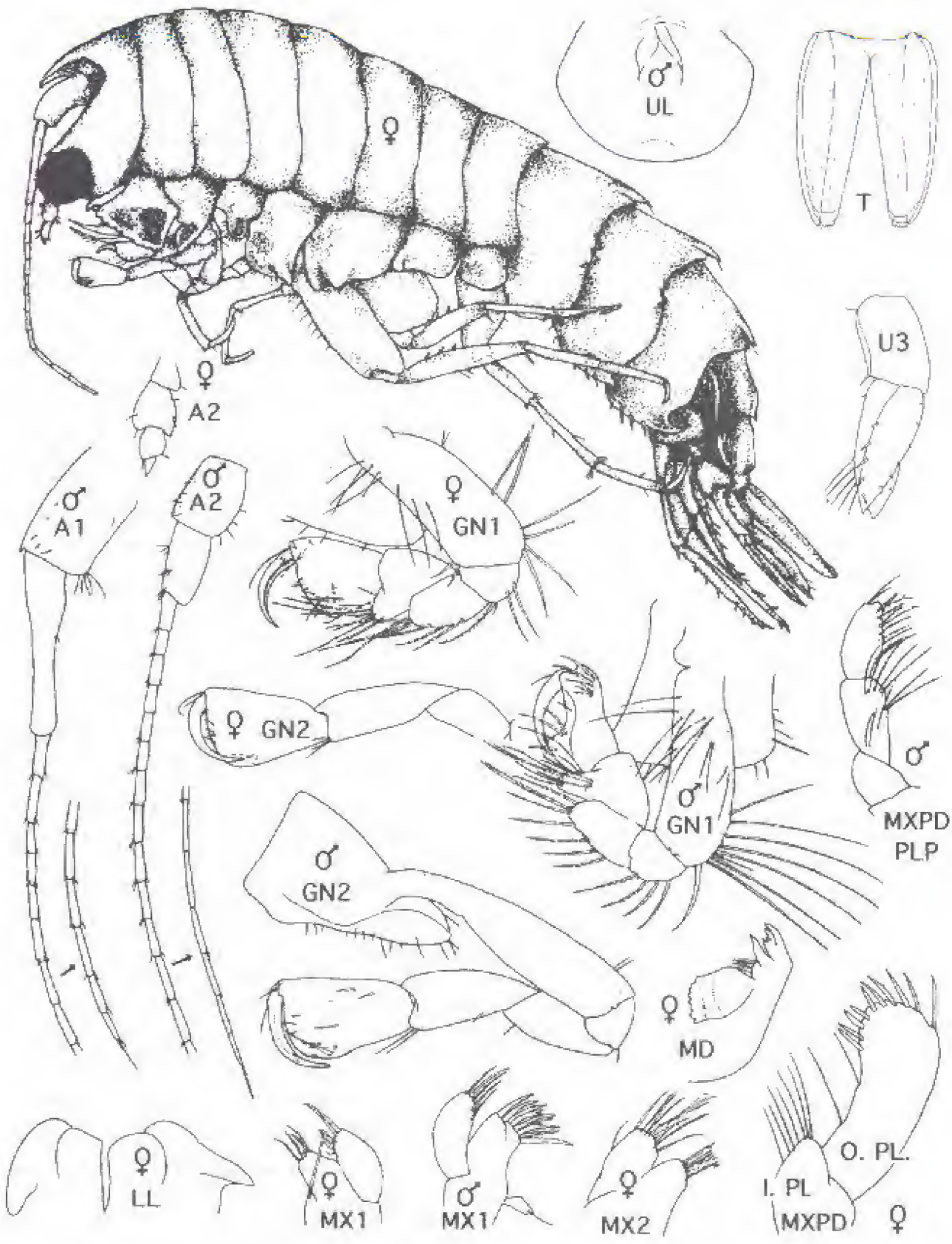


FIG. 26. ***Dexaminoculus grobbeni*** **(Spandl). Female (3.6 mm) Male (3.9 mm) Great Barrier Reef. (after Lowry, 1981).**

The genus was renamed and fully redescribed by Lowry (loc. cit.), based on more complete material from the Great Barrier Reef of Australia (Fig. 26). He likened it most closely to the genus *Dexaminella* Schellenberg (1928). On questionable grounds, Barnard & Karaman (1991) placed the genus within their realigned subfamily Prophliantinae. However, as Lowry (loc. cit.) and Ishimaru (1987) concluded, the balance of character states of *Dexaminoculus* are closer to the true dexaminins, *Dexamine*, *Paradexamine* and especially *Dexaminella* (Figs. 2(c); 29). Particularly significant is the form of the coxal plates, pleon carination, and the sexually dimorphic gnathopod 1, as well as mouthpart morphology. However, the extreme location of the eye is non dexaminin, and the lack of subchelae on the peraeopods is non polycheriin. The authors therefore propose the new subfamily Dexaminoculinae to facilitate recognition of its distinctive, major, taxonomic differences.

Prophliantinae Nicholls
(see Fig. 2(d))

Prophliantidae: Nicholls, 1939: 312.—Barnard, 1969a: 432.—Bousfield, 1982: 278.—Ishimaru, 1994: 43.
Dexaminidae (part): Barnard, 1970a: 163.—Bellan-Santini, 1982: 212.
Dexaminidae (Prophliantinae) Barnard, 1970: 161;—Ishimaru, 1987: 1413.—Barnard & Karaman, 1991: 273.

Type genus: *Prophlias* Nicholls, 1939: 312.

Genera: *Guernea* Chevreux, 1887: 302 (=*Prinassus*, =*Dexamonica*); *Haustoriopsis* Schellenberg, 1938:12.

Diagnosis: Body small, short, broad, surface often with rugose integument. Peraeon with low mid-dorsal carina (part or all), but no dorsal processes. Urosome segment 1 may be fused with fused segments 2 & 3. Rostrum very short. Anterior head lobe mainly rounded. Eyes pigmented, medium. Antenna 1 (female) short, peduncular segment 2 shorter than 1. Accessory flagellum minute or lacking. Antenna 2 (female) short; in male, peduncle short, segment 4 broad, flagellum elongate.

Mouthparts modified. Lower lip, inner lobes distinct. Mandible; molar variously reduced or modified; spine row lacking. Maxilla 1, palp 1(2) segmented; outer plate with 7-9 apical spines. Maxilla 2, plates modified, reduced. Maxilliped, outer plate large, inner plate small, palp shortened.

Coxae 1-4 slender, deep; coxa 1 shortest. Coxa 5 very large. Gnathopods slender, weakly subchelate; carpus usually longer than propod; palmar margins small, distinct.. Gnathopod 1, propod not sexually dimorphic.

Peraeopods 3 & 4 simple, not subchelate, segment 5 not strongly shortened. Peraeopods 5-7 short, generally dissimilar in form but little in size (peraeopod 7 shortest); bases variously broadened, unlike; segment 5 little shortened, often broadened; dactyls simple, short to medium.

Pleopods small; peduncle broadened, rami short. Uropods 1 & 2 short, rami usually unequal in length. Uropod 3 short, margins spinose (weakly setose in male).

Telson lobes medium, separated nearly to base, not diverging, apices truncate, spinose.

Coxal gills simple, not strongly pleated or lobate, on peraeopods 2-6 only. Brood plates small, linear, with apical setae.

Taxonomic Commentary: The authors concur with the decision of Barnard (1970a,) followed by Hirayama (1984, 1986), to transfer *Guernea* from family Dexaminidae to the Prophliantinae. Cluster analysis (p. 56, Fig. 29) further confirms its relatively close morphological similarity to *Prophlias* and *Haustoriopsis*. *Guernea* is a complex of diverse species groupings, some of which have been given formal generic and/or subgeneric status (*Prinassus* in the N. Pacific region and *Guernea* elsewhere). However, the authors also agree with the decision of Bellan-Santini (1983) and Ishimaru (1987) to resubmerge the names *Prinassus* and *Dexamonica* in the synonomy of *Guernea* Chevereux, 1887.

Barnard and Karaman (1991, loc. cit.) reduced the Prophliantidae to subfamily status within the Dexaminidae. This decision is supported by the present analysis (p. 56). As noted by Ishimaru (1987), those two authors also relegated the genus *Dexaminoculus* to the Prophliantinae on dubious grounds, and as noted here, without suitable concordance with their own subfamily diagnoses. The coral-dwelling *Dexaminoculus* is here considered distinctive at subfamily level (above). In balance, its phyletic affinities are closest to the primitive, nestling Dexamininae, and rather remote from the fossorially specialized and apomorphic Prophliantinae.

Guernea Chevreux

Guernea Chevreux, 1887b: 302.—Stebbing, 1906: 521 (part).—Barnard, 1970a: 11, figs.—Hirayama, 1985: 395.—Bellan-Santini, 1982: 225.—Ishimaru, 1987: 1395.—Ishimaru, 1994: 43.
Guernea (Guernea) J. L. Barnard, 1970a: 169.—Hirayama, 1985: 1.—Hirayama, 1986: 488.—Barnard & Karaman, 1991: 274.
Prinassus Hansen, 1888: 82.
Guernea (Prinassus) J. L. Barnard 1970a: 169.—Hirayama, 1985: 8.—Hirayama, 1986a: 493.—Barnard & Karaman, 1991: 275.
Dexamonica J. L. Barnard, 1958: 130, pls. 26-27.—Barnard, 1969a: 203.

Type Species: *Helleria coalita* Norman, 1868.

Species: About 24 described species and subspecies world-wide (Barnard & Karaman, 1991, updated). The following 11 species are recorded from the North Pacific region: *G. ezoensis* Ishimaru, 1987; *G. longidactyla* Hirayama, 1986a; *G. mackiei* Hirayama, 1986a; *G. magnaphilostoma* Hirayama, 1985; *G. minor* Ishimaru 1987; *G. nullispina* Hirayama, 1885; *G. quadrispinosa* Stephensen, 1944; *G. rectocephalus* Hirayama, 1985; *G. reduncans* J. L. Barnard, 1958; *G. sombati* Hirayama, 1986a; *G. terelamina* Hirayama, 1985; *G. tomiokaensis* Hirayama, 1985.

Diagnosis: Posterior peraeon and all pleon segments weakly carinated and/or posteriorly mucronate. Urosomite 1 separate, with mid-dorsal keel or hump (both sexes). Urosomites 2 & 3 coalesced, variously with small dorsal spines. Rostrum very short; anterior head lobe sharply rounded. Eyes medium, rounded, weakly faceted. Antennae (female) short. Antenna 1, flagellum 4-8 segmented; accessory flagellum minute or lacking.

Lower lip large, outer lobes with prominent shoulder cones. Mandibular molar variously triturative, often complexly divided; left lacinia 4(5) dentate. Maxilla 1, palp 1(2)-segmented, outer plate with 7-9 apical spines, inner plate 0(1)-setose. Maxilla 2, inner plate small, 2-5 setose. Maxilliped, inner plate very short, apex with 2-5 long setae; outer plate large, palp 4-segmented, dactyl short.

Coxae 1-4 medium, narrow, strongly overlapping, rounded below. Coxa 5 very large, deep, -postero-lobate. Gnathopods 1 slightly smaller than 2, basis with distinct proximal "buccal bend"; carpus relatively short and deep, little longer than propod; palm distinct.

Peraeopods 3 & 4, segment 5 shorter than 4 & 6, posterior margin spinose; dactyls medium. Peraeopods 5-6 subsimilar in form and length; segment 5 not shortened, dactyls various, usually reversed. Peraeopod 7, basis very broad; segments 4 & 5 broadened (not greatly, and/or asymmetrically, as in *Haustoriopsis*), margins strongly setose; dactyl short.

Pleon plates 1-3, hind corners rounded, or squared. Uropods 1 & 2, outer ramus the longer (usually), apices with long apical spine. Uropod 3, rami short, subequal, inner margins spinose (setose in male). Telson lobes medium, not diverging, outer margin and apex variously armed with setae and/or spines.

Distribution: Mainly tropical and warm-temperate (Indo-Pacific and tethyan) coastal shallows; fossorial in fine sediments. Of the 24 species and subspecies described to date world-wide, 12 (one-half) have been recorded from the North Pacific region, but only one of these from the North American Pacific coast.

Taxonomic Commentary: In balance of character states, *Guernea* appears more closely related to the type genus *Prophlias* than to the more highly specialized genus *Haustoriopsis*. It differs from *Prophlias*, however, in its stronger gnathopods, unexpanded segment 4 of peraeopod 5, and its dorsally carinated, unfused urosome segment 1.

Guernea reduncans (J. L. Barnard)
(Fig. 27)

Dexamonica reduncans J. L. Barnard, 1958: 130, pls. 26, 27.—Staude, 1987: 382.
Guernea (Prinassus) reduncans Barnard, 1970a: 173, figs. 1-3—Barnard & Karaman, 1991: 275.
Guernea reduncans Austin, 1985: 604.

Material Examined:
BRITISH COLUMBIA: Queen Charlotte Islands, ELB Stns. 1957: H4a mouth of Yakoun Bay, July 19 - 1 female with juveniles); W11, Head of Gudal Bay, Graham I., July 28 - 1 imm.
Vancouver I., ELB Stn. B27, Dodger Channel, SW end Diana I., July 8, 1976 - 1 male, 1 female ov. Off McCauley, Pt., Victoria, B. C., G. W. O'Connell Stns., Aug. 28, 1976: W10B - 1 male; W156B - 1 male , 3 females (ov) (fig'd. specimens). Off Victoria, C. Low coll., Aug., 1981 - 3 males, 5 females, 10 imm.

Diagnosis: Female ov. (2.4 mm); male (2.5 mm). Peraeon segments 6 & 7, and pleon segment 1-3 with low mid-dorsal ridge, slightly acute behind. Urosomite 2 with recurved mid-dorsal carina. Fused urosomites 2 & 3 somewhat humped mid-dorsally, with 2-4 small spines. Eye medium, subovate, about 25-faceted. Antenna 1, flagellum 5-segmented; peduncular segments 1-3 (male), anterior margins minutely crenulated; segment 1 deep, posterior margin distally with clusters of longish brush setae. Antenna 2, flagellum 3-segmented; flagellum (male) elongate (20+ segments), peduncular segments 4 & 5 enlarged, anterior margin of 4 with clusters of short brush setae.

Mandible, grinding surface of molar modified but entire, distal plumose seta short; left lacinia 4-dentate. Maxilla 1, outer plate with 7 apical spines; palp 1-segmented, apex with 2 setae. Maxilla 2, inner plate narrow, with 5 marginal setae. Maxilliped, inner plate with 3 long apical setae; palp segment 3 and short dactyl exceeding tall outer plate.

Coxae 1-4, lower margins finely crenulate and weakly setose. Coxa 5, anterior lobe small rounded, hind lobe very large, deeply rounded. Gnathopod 1, carpus and propod relatively short, deep, subequal in length; propod widening distally to convex palm, with 3-4 postero-distal spines. Gnathopod 2 slightly larger than gnathopod 1; carpus and propod slightly more slender and elongate; palm of propod with 3 postero-distal spines.

Peraeopods 3 & 4, segment 5 distinctly shorter than 4 & 5, hind margin with 3 stout spines increasing distally; dactyls medium. Peraeopods 5 & 6, segments 5, 6, and dactyls reversed; basis of peraeopod 5, hind lobe not strongly produced below; segment 4 normally broadened. Peraeopod 6,

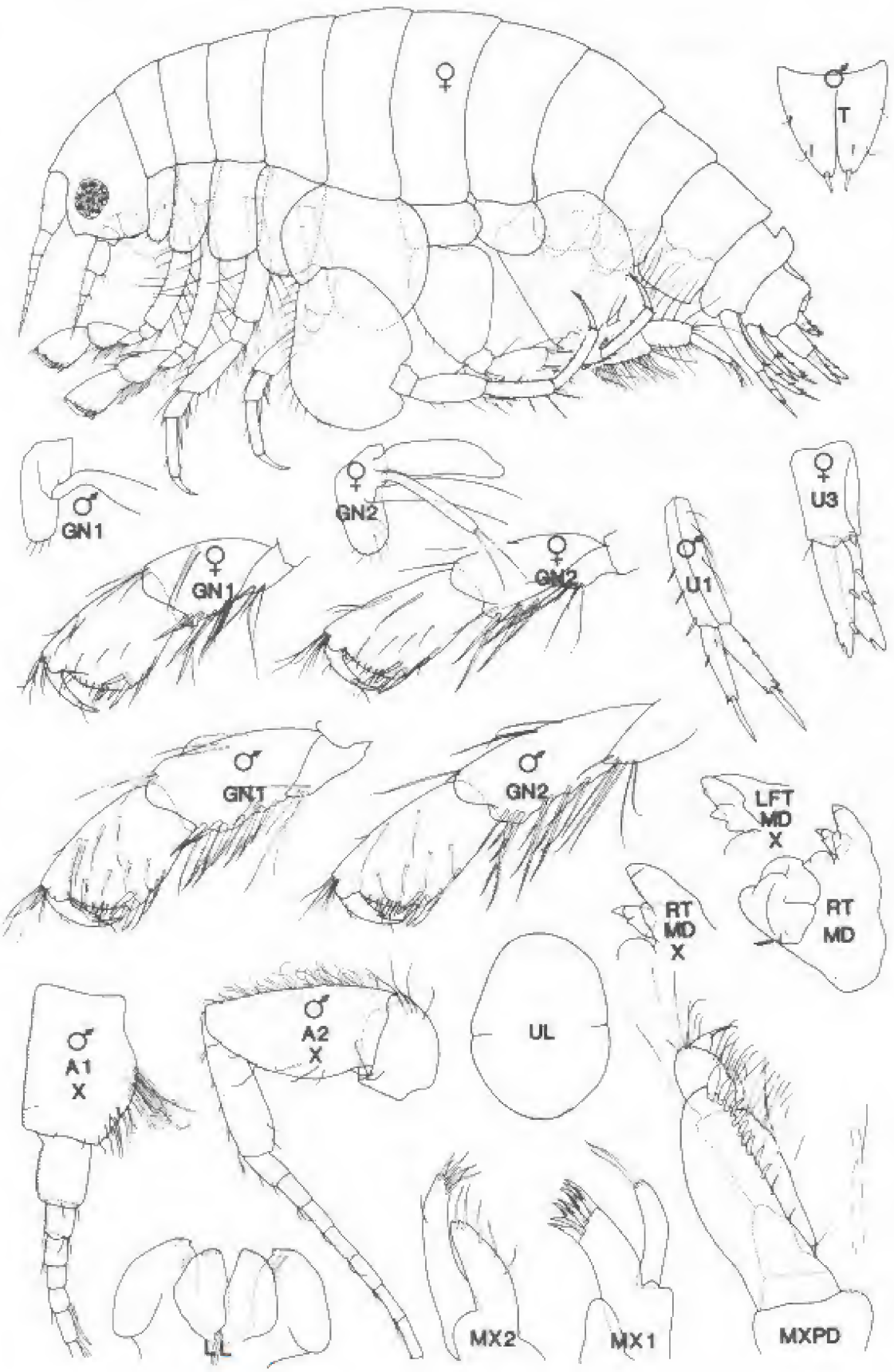


FIG. 27. Guernea reduncans (Barnard). Off Clover Pt., B. C. Fem. (2.3 mm) Male (2.0 mm)

basis narrowing distally, hind margin nearly straight, not markedly concave. Peraeopod 7, segments 4 & 5 not exceptionally broadened, length of each greater than width; dactyl slender, medium.

Pleon plates 2 & 3, hind corners squarish or rounded, lower margins weakly setose. Uropod 1, tips of rami exceeding uropod 2 but not uropod 3; peduncle with 3-4 proximal outer facial setae. Uropod 2, outer ramus the longer, apical spine about 2/3 its length. Uropod 3, rami about 50% longer than peduncle, margins with a few stout spines; in male, inner margin or both rami are plumose-setose.

Telson not longer than wide, lobes fused basally, submarginally with penicillate setae, apices each with single spine.

Distribution: Southern British Columbia, Washington and Oregon, to southern California, subtidally to about 100 m. in depth, in fine sand and muddy sand. The present records are the first authentically from British Columbia.

Taxonomic Commentary: The species apparently varies somewhat throughout its range. Material from California, illustrated by Barnard (1970a, loc. cit), exhibits distinct, posteriorly mucronate, peraeonal and pleonal carinations, and more elevated dorsal tooth on urosomite 1. Urosomites 2 & 3 bear 6 (vs. 2-4) dorsal spines, and apical spines of the uropod rami are longer. In southern material, the eye of the female is smaller, the flagellum of antenna 1 is 6- (vs. 5-) segmented, the posterior spines of segment 5 of peraeopods 3 & 4 are longer, the posterior lobe of the basis of peraeopod 5 is deeper and, in peraeopod 7, segment 5 is shorter and broader. Moreover, in maxilla 1 of Californian material, the palp has a weak suture dividing it into two segments, the outer plate bears 8 apical spines, and the inner plate a single apical seta. In males, the eye of northern material is larger with more numerous ommatidia.

Guernea reduncans appears more closely similar to *G. coalita* and *G. nordenskioldi* of the North Atlantic region than to species of the western Pacific described and figured by Hirayama (1985, 1986a) and Ishimaru (1987) (see below).

WESTERN N. PACIFIC SPECIES OF *GUERNEA*

To date eleven species of *Guernea* have been recrded and/or newly described from Asiatic North Pacific localities, as follows:

I. Sea of Japan Sea, Russian Coast.

1. *Guernea* species (identified as *G. nordenskioldi* by Bulycheva, 1955).

II. Coast of Hokkaido (material of Ishimaru, 1987).

2. *Guernea ezoensis* (males, females) - Otsuchi, Notsuke peninsula.
3. *G. minor* (males, females) - Shirahama.

II. West Kyushu coast, Japan (material of Hirayama, 1985):

4. *Guernea magnaphilostoma* (males, females) - Ariake Sea.
5. *G. terelamina* (female) - Shijiki Bay.
6. *G. tomiokaensis* (females, males) - Tomioka Bay.
7. *G. nullispina* (male, immatures) - Tomioka Bay.
8. *G. rectocephala* (females) - Tomioka Bay.

III. China Sea Coast (material of Stephensen, 1944).

9. *Guernea quadrispinosa* (male) - Liao-tung peninsula.

IV. Hong Kong (material of Hirayama, 1986).

10. *G.uernea sombati* (male, female).
11. *G. longidactyla* (male).
12. *G. mackiei* (males, females).

Taxonomic Commentary: The above species from the Japan and China Seas exhibit a considerable range of morphological diversity. However, a reasonably close perusal of illustrated character states did not reveal well-defined subgroups but rather a series of morphological specializations that presumably adapt each species for a particular niche and life style. The species range phyletically from the relatively primitive *G. ezoensis*, in which most character states are plesiomorphic, to the highly specialized minute species, *G. minor*, in which most character states are apomorphic. None closely resembles the type species, *G. coalita* (Norman) from the North Atlantic region, but differs especially in the form of the gnathopods, and in the shape of the mid-dorsal process of urosome 1. Barnard (1970a) has previously commented on differences between the material of Bulycheva (1955) from the Japan Sea (No. 1, above), and his material of *G. nordenskioldi* from North Atlantic coastal regions, and of *G. reduncansmns* from California. The last two species were both fully illustrated in his extensive generic revision (Barnard, 1970a).

A key to North Pacific species is beyond the scope of this study. However, *G. reduncans* was found to differ from species Nos. 2, 6, and 10 in which the outer plate of maxilla 1 has 9 apical spines; from Nos. 3, 5, 7, 8, and 12 in which the outer ramus of uropod 3 lacks plumose swimming setae in the male; and from No. 9 in which the apical spines of the rami of uropods 1 & 2 are extremely long. *G. reduncans* differs perhaps least from Nos. 4 & 11 (above) but both the latter species have relatively slender gnathopods, and telson lobes that are marginally and/or apically setose. Hopefully, this study may stimulate a thorough revision of this challenging assemblage of western Pacific prophliantids.

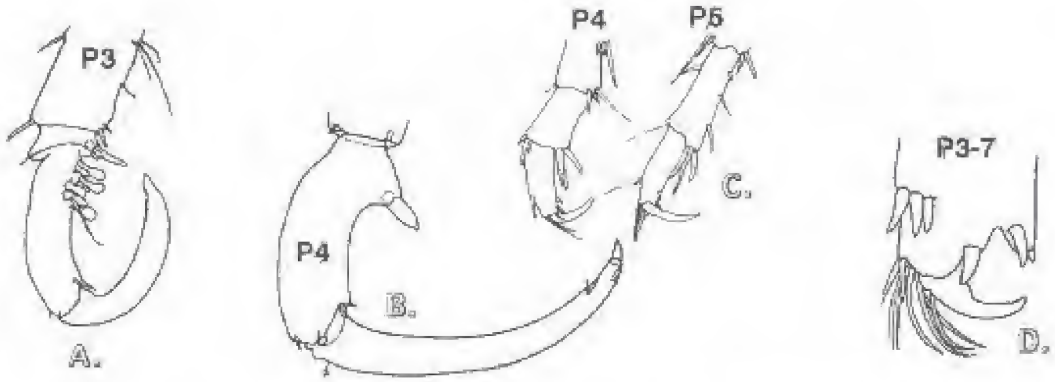


FIG. 28. Prehensile Peraeopods in Dexaminoidea (modified partly from Vader, 1983)

A. Nototropis falcatus B. Delkarlye enamalla C. Tritaeta gibbosa D. Polycheria obtusa

Discussion and Conclusions.

This study treats the systematics and distributional ecology of some 12 species of dexaminoidean amphipod crustaceans occurring in North American Pacific coastal marine waters, from the Bering Sea to Northern California. This fauna is small and relatively minor in contrast to several large and diverse regional gammaridean superfamilies previously treated (e.g. Gammaroidea (Bousfield, 1979); Ampeliscoidea (Dickinson, 1982, 1983); Corophioidea (Conlan, 1983); Phoxocephaloidea (Jarrett & Bousfield, 1994), and others of this series now in preparation (e.g. Talitroidea, Eusiroidea, Hadziodea (Bousfield Staude, 1994). Moreover, regional dexaminoideans include only about 7% of the ~200 species described to date, world-wide. However, this small fauna is remarkable in containing: (1) a large component of the single most primitive subgroup, the subfamily Atylinae; (2) significant representation from the most advanced subfamily, the Polycheriinae; (3) only one species from the other six phyletically intermediate subfamily groups. Thus, in combination with counterpart dexaminoidean groups from the Asiatic North Pacific coastal marine region, this modest North American assemblage makes up in taxonomic and phyletic quality what it lacks in species numbers, and thereby provides a basis for review and reclassification of the entire world fauna not previously realized.

Natural relationships among species and generic groups are here tested more critically by means of a modification of the phenetic UPGMA (cluster analysis) system of Sneath and Sokal (1973). The modified but relatively unsophisticated system employs an overall criterion of phyletic similarity termed the Plesio-Apomorphic (P.-A.) Index in which low numbers signify phyletically primitive, and high numbers advanced, taxonomic groups. The system has been utilized effectively in similar studies by Conlan (1983), Staude (1986) and Jarrett and Bousfield (1994). Within the superfamily Dexaminoidea, analysis of generic similarities is based on 21 characters and corresponding 42 character states given in Table I (p. 57). The lepechinellids are here represented pragmatically by one genus, *Lepechinella*, mainly because it contains more than 90% of the species, and the three other described genera do not show differences (from it) in the character states utilized in this analysis.

The resulting phenogram (Fig. 29) "clusters out" two main subgroupings at less than 50% similarity, viz. a primitive, thin-bodied, atylid family group (with P. A. indices of 9-24) on the left, and a relatively advanced, broad-bodied, dexaminid family group (with P.-A. indices of 15-29) on the right. The atylids are especially primitive in retaining a number of presumed ancestral features (e.g. Bousfield, 1983) such as basic body carination, peraeopods, pleopods, mouthparts, and pleated gill structure, whereas the dexaminoideans tend more strongly to reduction or loss of body carination, mouthpart armature, and modification of the peraeopods towards "prehensility" on the one hand (Fig.28, above) or fossorial life style on the other (Fig. 2 (d), p. 7).

Within the Atylidae, four subgroups "cluster out" with paired character state similarities between 60 and 75%, that are here recognized at subfamily level. These include the very primitive large-bodied Atylinae (P.-A. Index of 9) on the one hand, and the advanced, small-bodied Anatylinae (P.- A. Index of 22-24) on the other. The other two groups, Nototropiinae and Lepechinellinae, intermediate in body size and phyletic positioning (P. A. indices of 16-19), trend to a more free-living, epibenthic and pelagic life style, with strong deep-water and abyssal components. The biogeographical significance of these phyletic relationships is noted below (p. 60).

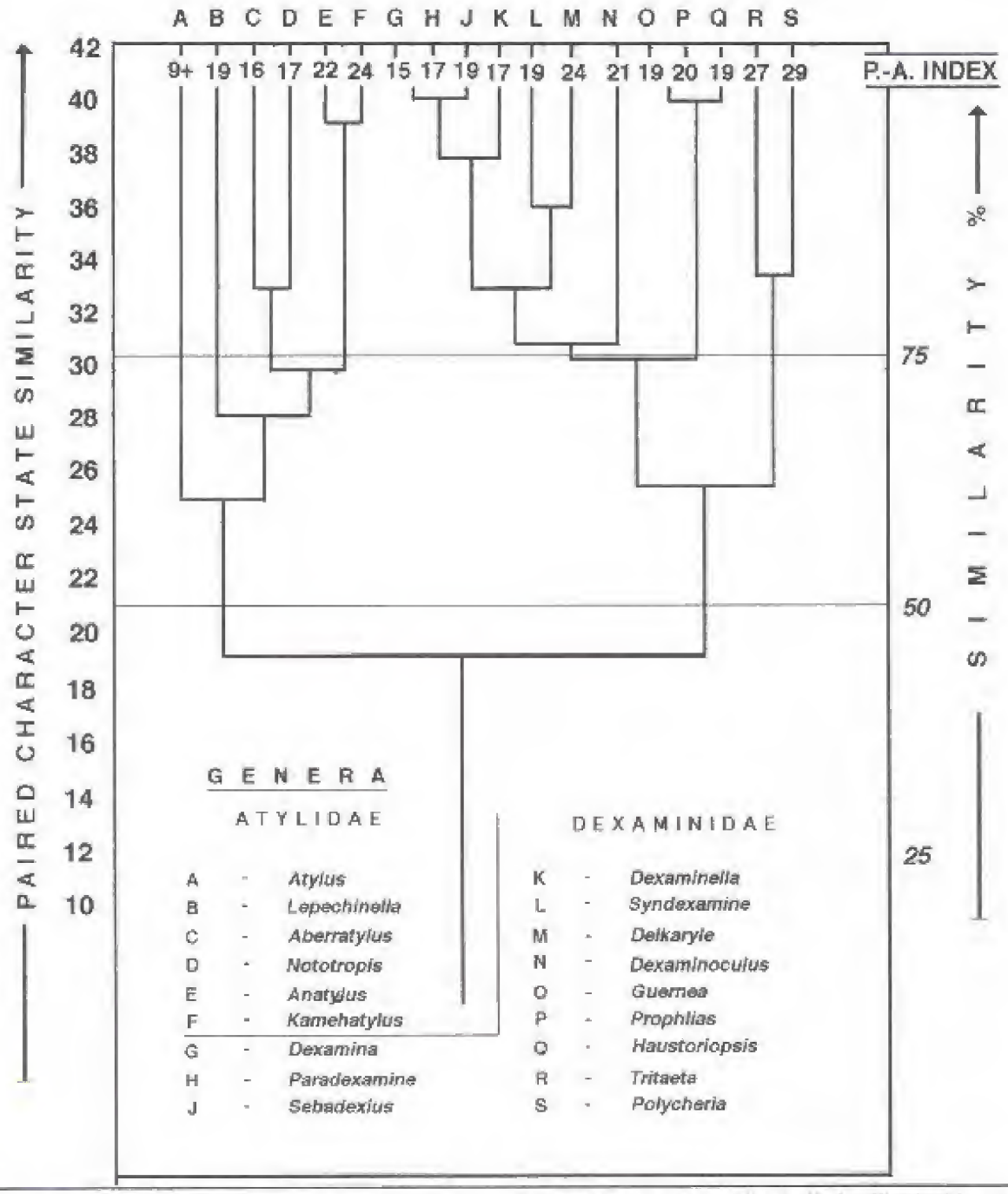
Within family Dexaminidae, containing nearly twice the number of genera, four subfamily groupings are similarly recognized. These "cluster out" at slightly higher levels of character state similarity (60-77%). These subfamily groupings include the relatively primitive Dexamininae containing six relatively similar genera (P. A. indices of 15-24) on the left, and the advanced, highly specialized and commensal pair of genera comprising the Polycheriinae (P. A. indices of 27-29) on the right. The two phyletically intermediate subgroups (P. A. Indices of 19-21) encompass two subfamilies of widely differing morphologies and life styles, viz. the monotypic, coral-dwelling Dexaminoculinae, on the

TABLE I. GENERA OF DEXAMINOIDEA: CHARACTERS AND CHARACTER STATES

CHARACTER	CHARACTER STATE VALUE		
	Plesiomorphic	Intermediate	Apomorphic
	0	1	2
1. Rostrum	long	medium	short
2. Body form	very slender		short and stout
3. Thorax, dorsum	spinose		not spinose
4. Accessory flagellum	1-segmented	minute	lacking
5. Sexual dimorphism of antennae, gnathopds	strong		weak or none
6. Mandibular palp	present, strong	weak	lacking
7. Mandibular molar	large, triturative		non-triturative
8. Lower lip, inner lobes	lacking	weak	well developed
9. Maxilla 1, palp	2-segmented		1-segmented
10. Maxilliped palp	4-segmented		3-segmented
11. Coxal plates 1-4	smallest anteriorly		deepest anteriorly
12. Coxal plate 5	shallow		deep (about = 4)
13. Gnathopods 1 & 2, propod & carpus	elongate		short & deep
14. Peraeopods 3 & 4	simplidactylate.		subchelate
15. Peraeopods 3 & 4, . length of segment 5	> segment 4	< segment 4	<< segment 4
16. Peraeopods 5-7, width basis	broad, suborbicular		narrow
17. Peraeopods 5-7, similarity	similar in size and form	unlike in size or form	unlike in size and form
18. Pleon, dorso-lateral armature	toothed		smooth (or nearly so)
19. Urosome 5 & 6, dorso-lateral "wings"	present	weak	lacking
20. Uropod 3, rami	lanceolate; margins plumose-setose		linear; margins spinose
21. Telson lobes	separate, converging		basally fused

one hand, and a complex of three small bodied, fossorial genera within the Prophliantinae on the other. The Dexaminoculinae and Polycheriinae are linked naturally to the Dexamininae by greater overall character state similarity of the peraeopods and most other body appendages, including similar sexual dimorphism of the propod of gnathopod 1, apparently unique to this family within all gammaridean amphipod superfamilies (Fig. 2, p. 7). Close comparison of individual character states suggests that the Prophliantinae differ from the Dexamininae somewhat more strongly than semi-phyletic numerical taxonomic methodology actually reveals. This methodology may be arguably more susceptible to homoplasious or convergent similarities than cladistic analytical methodology. A broader cladistic analysis, not

FIG. 29. DEXAMINOIDEA: PHENOGRAM OF GENERA.



attempted in this regional study, may show greater phyletic significance to the differences, especially in gnathopod structure, and perhaps justify restoration of the Prophliantins to family level of recognition.

Within the monotypic genus *Atylus* (subfamily Atylinae), an amphi-North Pacific near-total assemblage of 10 species may be phenetically analyzed, based on 20 characters and character states outlined in Table II. The resulting phenogram (Fig. 30, p. 60) encompasses two not very closely similar subgroups, a primitive large bodied *carinatus-levidensus* assemblage (P. A. Indices of 10-21) on the left, and a more advanced, generally smaller bodied *collingi-tridens* assemblage (P. A. indices of 20-33) on the right. The most primitive members of the *carinatus* subgroup, *A. carinatus* and *atlassovi*, appear not far removed in basic morphology from large regionally occurring gammaroidean amphipods (e.g. various Anisogammaridae, and the *Gammarus setosus -wilkitzkii* complex within family Gammaridae: see Bousfield, 1979). Within the *A. levidensus* subcomplex, including *A. eknani* and *A. bruggeni* , some reduction of mouthparts (e.g. mandibular palp) and specialization of body appendages (e.g. pectinate setation of gnathopod

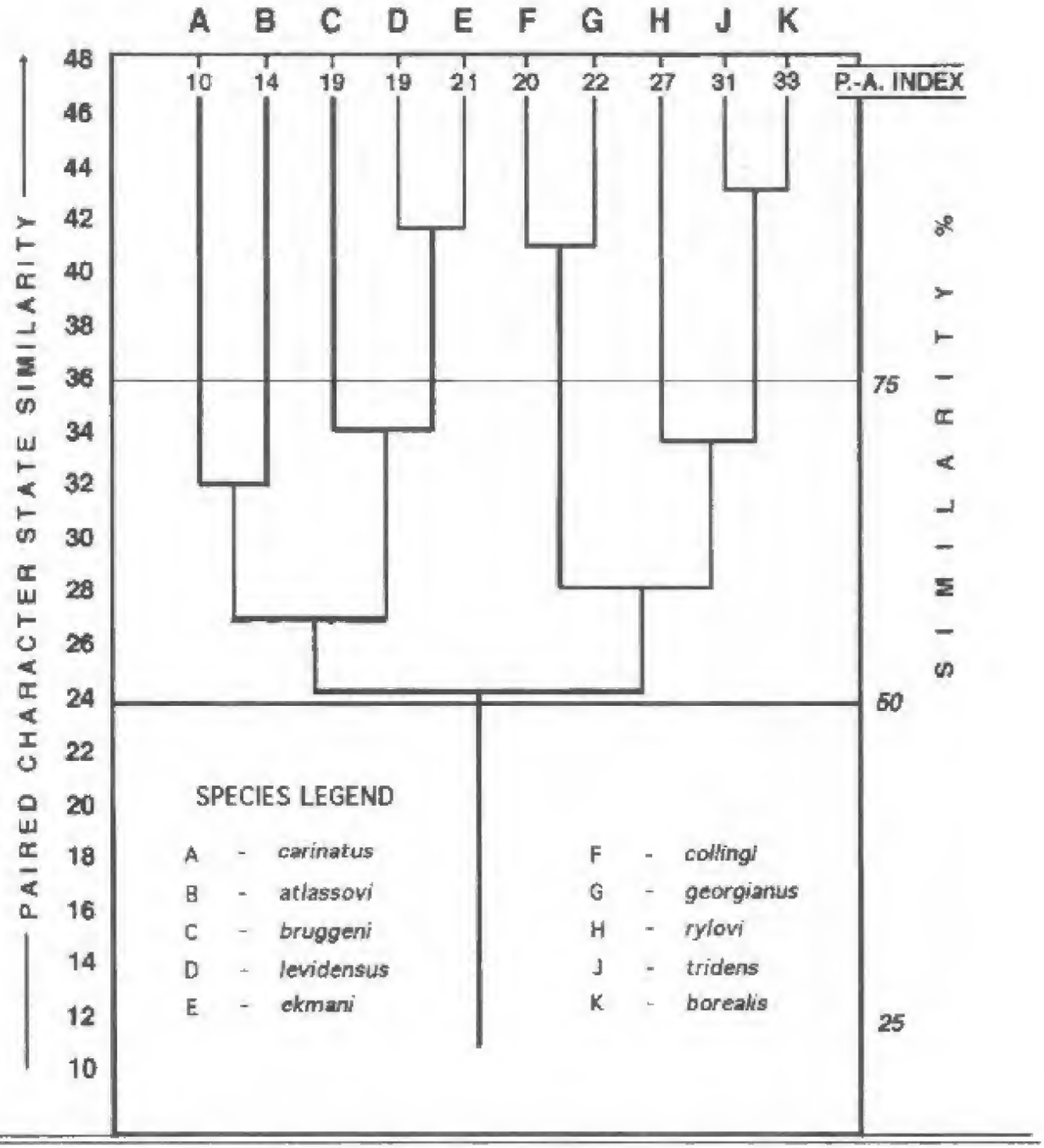
TABLE II. SPECIES OF *ATYLUS:* CHARACTERS AND CHARACTER STATES.

CHARACTER	CHARACTER STATE VALUE		
	Plesiomorphic	Intermediate	Apomorphic
	0	1	2
1. Body form	very slender		short and stout
2. Thorax, dorsum	spinose		not spinose
3. Accessory flagellum	1-segmented, minute		lacking
4. Sexual dimorphism of antennae, gnathopods	strong		weak or none
5. Mandibular palp	present, strong	weak	lacking
6. Mandibular molar	large, triturative		non-triturative
7. Lower lip, inner lobes	lacking	weak	well developed
8. Maxilla 1, palp	2-segmented		1-segmented
9. Maxilliped palp	4-segmented		3-segmented
10. Coxal plates 1-4	smallest anteriorly		deepest anteriorly
11. Coxal plate 5	shallow,		deep (about = 4),
12. Gnathopods 1 & 2, propod & carpus	elongate		short & deep
13. Peraeopods 3 & 4	simplidactylate.		subchelate
14. Peraeopods 3 & 4, length of segment 5	> segment 4	< segment 4	<< segment 4
15. Peraeopods 5-7, width basis	broad, suborbicular		narrow
16. Peraeopods 5-7, similarity	similar in size and. form	unlike in size or form	unlike in size and form
17. Pleon, dorso-lateral armature	toothed		smooth (or nearly so)
18. Urosome 5 & 6, dorso-lateral "wings"	present	weak	lacking
19. Uropod 3, rami	lanceolate; margins plumose-setose		linear; margins spinose
20. Telson lobes	separate, converging or straight.		basally fused, spreading

propods) is evident (Fig. 7). Within the *collingi* group, the more advanced *tridens* subgroup exhibits weakest body carination, and most strongly modified peraeopods in which character states trend, probably convergently, with comparable features of the Nototropiinae (Fig. 1(b)).

The North Pacific species of the highly specialized genus *Polycheria* (dexaminid subfamily Polycheriinae) may also be analyzed numerically on the basis of 20 characters and corresponding character states outlined in Table III (p. 61). Character states of the *P. antarctica* complex of species of southern oceans is included here for broader perspective on morphological relationships within the genus. The resulting phenogram (Fig. 31, p. 62) "clusters out" two major subgroups, a primitive *japonica* subgrouping of three west-

FIG. 30. PHENOGRAM OF SPECIES OF *ATYLUS*



ern Pacific species (P. A. indices of 8-19) on the left, and a highly advanced *osborni* subgroup (P. A. Indices of 26-28) on the left. The *osborni* subgroup exhibits significantly greater reduction of mouthparts and specialization of coxal plates, peraeopods, and uropods, differences perhaps related to differing life styles in association with differing host organisms.

Although the combined North Pacific and *Polycheria antarctica* assemblages, in toto, represent only about one-third of the world-wide fauna, some tentative inferences may be drawn. The North American and Asiatic subgroups differ very significantly from each other, clustering at less than 50% similarity, and perhaps meriting separate generic (certainly subgeneric) recognition of the North American assemblage. Such would seem further justified by the fact that the *antarctica* subgroup, closer to the generic type *P. tenuipes* Haswell from southern oceans, clusters much more closely with the Asiatic than with the North American Pacific *osborni* group . Hopefully, this limited study will point the way to a more broadly based solution to phylctic relationships and formal classification within subfamily Polycheriinae.

TABLE III. SPECIES OF *POLYCHERIA*: CHARACTERS AND CHARACTER STATES

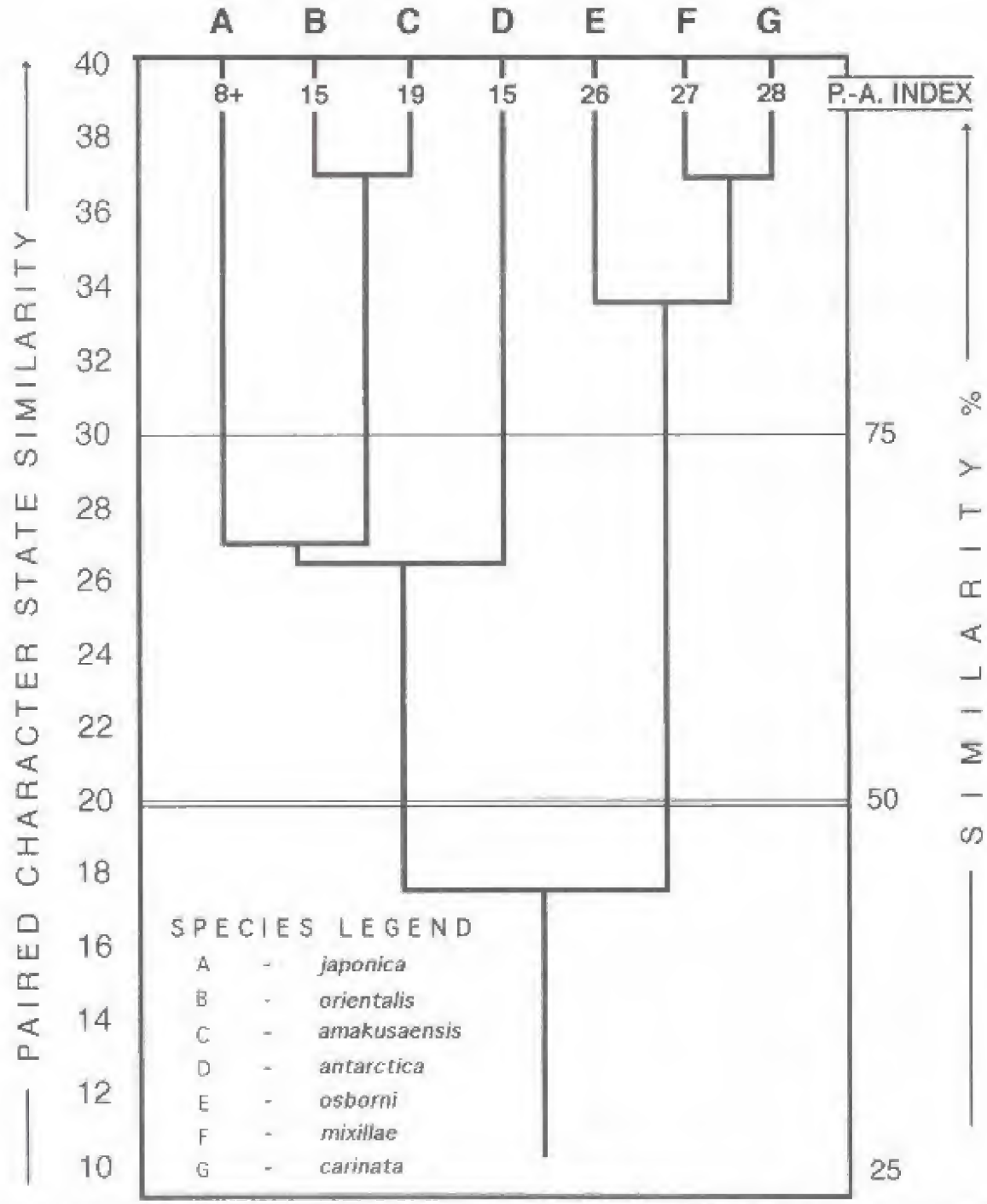
CHARACTER	CHARACTER STATE VALUE		
	Plesiomorphic	Intermediate	Apomorphic
	0	1	2
1. Antenna 1, segment 3 length	> flagellar segm't	= flag. segm't	< flag. segm't
2. Mandible: number of blades in spine row	4	3	1-2
3. Maxilla 1, number of outer plate spines	9		7
4. Maxilla 1, length of palp	exceeding outer plate	= outer plate	shorter than outer plate
5. Maxilla 2, inner plate, No. marginal setae	many (>10)	3-5	0-2
6. Maxilliped, length of palp	exceeding outer plate	= outer plate	shorter than outer plate
7. Coxae 1 & 2, lower margin	rounded	squared	front acute
8. Coxa 3, lower front corner	rounded	process small	process large
9. Gnathopod 1, palm of propod	long	medium	short
10. Gnathopod 2, palm of propod	long	medium	short
11. Peraeopods 3 & 4, length of segm't 5	> segm't 6	= segm't 6	< segm't 6
12. Peraeopods 5-7 length of segm't 5	> segm't 6	= segm't 6	< segm't 6
13. Peraeopod 7, width of basis (segm't 2)	broadened	sl. broad	sublinear
14. Peraeopods 5-7, length of segm't 5	>segm't 6	= segm't 6	< segm't 6
15. Urosomite 2 & 3 Number dorsal spines	numerous	4	0-2
16. Uropod 1, peduncular outer marginal setae	lacking	few	strong row
17. Uropod 2, length of inner ramus	> outer ramus	= outer ramus	< outer ramus
18. Uropod 3, length of rami (female)	subequal	slightly unequal	markedly unequal
19. Telson lobes, basal fusion	little (1/6)	intermediate	much (1/3-1/4)
20. Telson lobes, number of lateral spines	many 7-8	intermed.(4-6)	few (0-3

Biogeographic Considerations

The limited occurrence of Dexaminoidean amphipods in the North Pacific region allows for few broad conclusions concerning regional biogeography of the group. However, the regional and world-wide distributional record of component families and subfamilies, including the more diverse western North Pacific dexaminoidean fauna, is more helpful (see Table IV, p. 62). Less than 200 world species are encompassed by 22 genera and 8 subfamilies (columns 1, 2). The low species/genus ratio provides a relatively high index of morphological diversity within the superfamily and, by inference, a relatively long or ancient evolutionary history of the group as a whole.

Within family Atylidae, 3 subfamilies are mainly littoral and sublittoral (column 7), whereas the Lepechinellinae

FIG. 31. PHENOGRAM OF SPECIES OF *POLYCHERIA*



(containing nearly half the known atylid species) is abyssal, mainly in Indo-Pacific and Atlantic regions. The 11 species of subfamily Atylinae (*Atylus*) are endemic to the North Pacific region, with a single outlier in the Atlantic and one possibly in the Antarctic. By contrast, the 20 species of Nototropiinae are mainly Indo-Pacific and Atlantic, with a few outliers reaching the western Pacific. The little known subfamily Anatylinae is also mainly Indo-Pacific, with 2 species reaching the Sea of Japan but none attain the North American Pacific coast.

Within the more diverse and species-rich family Dexaminidae, all four subfamilies are primarily Indo-Pacific, and the few described species within subfamily Dexaminoculinae are endemic there. A few members of the primitive subfamily Dexamininae penetrate into temperate waters of the North Atlantic and southern Japan (Kyushu). Subfamily Prophliantinae is also Indo-Pacific and southern, but with stronger representation in the North Atlantic and western Pacific regions. By contrast, the phyletically most advanced subfamily, Polycheriinae, penetrates fairly strongly

TABLE IV. GEOGRAPHICAL DISTRIBUTION OF DEXAMINOIDEA*

TAXON	DIVERSITY		DISTRIBUTION				DEPTH ZONE*
	NO. GEN.	NO. SPP.	NORTH ASIATIC	PACIFIC N. AMER.	N. ATL.	INDO-PACIFIC	
ATYLINAE	1	11	X	X	x	x?	L-SL
NOTOTROPHINAE	2	~20	x	0	X	X	L(A)
LEPECH.'INAE	4	~34	X	x?	X	X	A
ANATYLINAE	2	4	X	0	0	X	L
DEXAMININAE	7	~55	X	0	X	X	L-SL
DEXAMINOC'INAE	1	1	0	0	0	X	L
POLYCHERIINAE	2	~24	X	X	x	X	L-SL
PROPHLIANTINAE	3	~40	X	x	X	X	L-SL
Totals	22	~190					
AMPELISCOIDEA	4	~230	X	X	X	X	L-A

* Data updated from Barnard & Karaman (1991).

*LEGEND: L - Littoral; SL - Sublittoral.; A - Abyssal.. X - common; x - species few; 0 - absent.

northwards along both Asiatic and North American Pacific coasts, with its most primitive members (within genus *Tritaeta)* confined to the Mediterranean and eastern North Atlantic regions.

With respect to local distribution, the North American Pacific coastal marine fauna here consists of 8 atylins, 3 polycheriins, and one prophliantin. Three species of lepechinellins occur at abyssal depths off the eastern Pacific continental slope, from Central America north to Baja and southern California but, to date, none has been recorded from off Oregon or points northward (Barnard, 1973; Barnard & Karaman, 1991). As noted previously in this text, of the 8 regional species of *Atylus*, three species within the more primitive *carinatus-levidensus* subgroup (i.e., *A. carinatus, A. atlassovi, and A. bruggeni*) do not extend south of the Bering Sea, and only *A. levidensus* reaches California. Within the advanced *collingi-tridens* subgroup, all four species occur in the central region of British Columbia. However, *A. tridens* and *A. georgianus* do not extend north to the Bering Sea, but occur southward to central California. Of seven atylin species recorded from coastal western Pacific waters, *A. ekmani, A. rylovi,* and *A. occidentaliss* (advanced morphological counterparts of *A. levidensus, A. tridens,* and *A. collingi*) also extend furthest southwards. The more southerly occurrence, in North American Pacific waters, of phyletically advanced members of major taxonomic units has been noted previously within subfamilies of the Phoxocephaloidea, especially subfamily Metharpiniinae (Jarrett and Bousfield, 1994) and subfamily Pleustinae within the Leucothoidea (Bousfield & Hendrycks, 1984). The evolutionary significance of this phenomenon is yet inconclusive, but possibly reflects the overall depressant effect of low temperatures on rates of evolution, all other factors being equal (Ekman, 1953).

The distribution of ampeliscoidean amphipods, considered to be close but more highly advanced and specialized phyletic counterparts of dexaminoideans, stands in marked contrast (Table IV). Through modifications of peraeopods 3-7, ampeliscoideans are able to construct and live (in the "upside down" fashion of polycheriins) within protective vertical tubes of their own construction. They thereby exploit, in vast numbers, the rich tryptonic and deposit food resources on and above sedimentary substrata. Ampeliscoideans occur abundantly along all marine coastlines, including the arctic and antarctic, but relatively few have penetrated the deep sea (Table IV, columns 3-6). However, relative to the dexaminoideans, the larger number of described species (column 2) is encompassed by only 4 genera and one subfamily (column 1), three-fourths in the essentially littoral-sublittoral genus *Ampelisca*. This high species/genus ratio implies a relatively low index of morphological diversity and a relatively recent evolutionary history. This difference would suggest that the Dexaminoidea is, palaeohistorically, an older superfamily group than the Ampeliscoidea. The most primitive members (e.g. of *Atylus*) now exist in phyletically relict or semi-relict fashion, still occupying marine "nestling" niches that gammaroideans and other more eurytopic and more successful ecological counterparts have apparently not yet penetrated.

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LEGEND FOR FIGURES

A1 - antenna 1; A2 - antenna 2; ABD - abdomen; ACC FL - accessory flagellum; BR - branchia (coxal gill); CX - coxa; EP - epimera (pleon plate); GN - gnathopod; HD - head; JV - juvenile; LL - lower lip; LFT - left; MD - mandible; MX - maxilla; MXPD - maxilliped; PL - pleopod; PLP - palp; RT - right; T - telson; UL - upper lip; U - uropod; UROS - urosome; X - enlarged; O - male; O - female.